

# Population dynamics in a guild of four Mediterranean ungulates: density-dependence, environmental effects and inter-specific interactions

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Population fluctuations in ungulates are driven by both intrinsic and extrinsic factors. Available information, however, mainly refers to arctic, temperate and African ungulate populations, while the dynamics of Mediterranean species, exposed to a milder climate, is known to a much lesser extent. Here we studied the population dynamics of four wild ungulate species in the Castelporziano Preserve near Rome, Italy, as obtained from detailed bag counts from hunting drives during the period 1878–1986: the Italian roe deer *Capreolus capreolus italicus*, the Maremma wild boar *Sus scrofa majori* (both endemic to Italy), the native red deer *Cervus elaphus*, and the alien fallow deer *Dama dama*. We also considered the effects of the presence of another alien ungulate, the nilgai *Boselaphus tragocamelus*.

This ungulate community experienced an accidental ‘removal experiment’ when, during World War II, red deer and nilgai were exterminated. This event and the length of the time series allowed us to test two main hypotheses: 1) that the complexity level of the ungulate community affects the strength of intra- and inter-specific competition; and 2) that in Mediterranean environments intra- and inter-specific interactions are stronger than climate forcing. Statistical methods ranged from state-space-modelling, GLM analysis and structural equation models.

The results indicated that direct intra-specific density dependence played a relevant role for all species, and was stronger after the removal. A complex pattern of species interactions was however revealed; fallow deer had a negative effect on roe deer population, while roe deer had an apparent positive effect on red deer and wild boar, possibly mediated by environmental factors. Nilgai appeared to facilitate all deer species. The results of the analysis also confirmed that at present climate appears to play a minor role with respect to density dependence; however, the increasing aridity of the Mediterranean area could change this picture in coming decades.

For a long time, ecology has witnessed a lively debate on the relative importance of intrinsic factors (intra-specific competition) and extrinsic effects such as environmental variations and inter-specific competition, in determining the dynamics of animal populations (Hixon et al. 2002). However, the distinction between the two sets of causes can be difficult, due to the complexity of interactions between density-dependence and climate, whose effects may vary for different demographic classes (Coulson et al. 2001, Owen-Smith 2010). In ungulates, in particular, it has been suggested that density-dependence first affects juvenile survival, then age at first breeding, thereafter adult fecundity, and finally adult survival (Eberhardt 2002).

Both temporal and spatial heterogeneity can affect the strength of density dependence (Wang et al. 2006), and Post (2005) showed that the strength of density-dependence declines from southern to northern latitudes in Fennoscandia. Arctic ungulates are strongly influenced by stochastic variation in climate (Aanes et al. 2000), as well as alpine

species and populations living in northern Europe (Jacobson et al. 2004, Mysterud and Østbye 2006).

Besides intra-specific relationship, population are influenced by sympatric species using similar resources. Farnsworth et al. (2002) showed that interactions among populations of grazers may result in competitive exclusion, coexistence or facilitation, depending on the way species partition resources and on the dynamics of resource renewal. In principle, we can envisage a negative effect of the presence of other large herbivores, as the result of inter-specific competition for food resources (Feldhamer and Armstrong 1993, Putman 1996, Yoshihara et al. 2008), but there are also evidences of non-competitive coexistence among ungulate species, and even facilitation (Bell 1971, Arsenault and Owen-Smith 2002), mediated by different resource use due to differences in mouth structure and body size (Prins and Olff 1998). Even though little is known about inter-specific interactions between Mediterranean ungulates, some observations suggest that roe deer suffers from competition with fallow deer

(Focardi et al. 2006, Ferretti et al. 2008). More specifically, Focardi et al. (2006) showed that the reduction of habitat quality by fallow deer negatively affects the phenotypic quality of Italian roe deer at Castelporziano. Competition and facilitation for resources are widely accepted as mechanisms driving the spatial distribution of ungulate assemblages (Sinclair and Norton-Griffiths 1979). However, evidence for competition or facilitation at population level (that is, a decrease in population abundance due to competition, or an increase due to facilitation) in herbivores communities remains meagre (Arsenault and Owen-Smith 2002).

The studies cited so far have considered arctic, temperate and African ungulate populations. At present, the population dynamics of Mediterranean species is poorly known. At variance with northern or semi-arid environments, the typical Mediterranean climate is characterized by mild winters, with almost no frost or snow, moderately warm summers and rather limited seasonal temperature variations. Thus it could be speculated that, for Mediterranean ungulates, density dependence and inter-specific interactions could be stronger than for species dwelling harsher environments.

In Mediterranean environments, the only important climatic factor is presumably associated with spring and summer precipitation, which is generally scarce and accompanied by warm conditions. Larger water availability during these months can be expected to positively affect the quantity of food available to female ungulates during late gestation and lactation. In particular, according to Gaillard et al. (2000), juvenile survival and fecundity of young females show considerable temporal variations in ungulates and are the key factors influencing changes in population numbers. Thus, we expect negative effects of intra-specific competition and spring-summer drought on the population growth rates of all species, through a negative influence on fecundity of primiparous females. For polycotous species showing sharp variations in litter size, such as wild boar and, at a lesser extent, roe deer, juvenile survival in summer could be important in determining population fluctuations. Therefore, we can hypothesize a negative influence of adverse weather conditions during the birth season: an excess of rainfall when most of the newborn piglets (in May) or fawns (in May–June for deer species) rest on the ground, could lead to problems in thermoregulation which may increase mortality (Van Moorter et al. 2009); we also expect that summer drought may negatively impact on the growth rate of these ungulate species. For wild boar, a positive influence of rainfall on pregnancy rate and litter size was described by Fernandez-Llario and Mateos-Quesada (2005), while Focardi et al. (2008) found limited effects of climate on juvenile survival.

In this paper, we investigated the population dynamics of four ungulate species inhabiting a Mediterranean environment by the analysis of long-term time series, obtained from bag records collected in the Castelporziano Preserve, near Rome, Italy (Imperio et al. 2010). The peculiarity of wildlife management in the Preserve and the detailed hunting records allowed us to reconstruct the densities of all ungulate species for a period of 109 years (1878–1986), as well as the hunting effort. It is well known that hunting data cannot be used as a proxy for population density without any previous assessment of their validity (Ranta et al. 2008). However, the time series of Castelporziano hunting data on ungulates

show a good agreement with count data and are not affected by hunter's habitat selection (Imperio et al. 2010). Even so, observation error can be still present, thus we Kalman-filtered the original time series using a linear state-space approach (Dennis et al. 2006). Climate data were available for the whole study period, and a sequence of map/aerial photographs allowed for reconstruction of habitat variations in time.

From 1889 to 1943, five species of ungulates coexisted at medium-high densities: Italian roe deer *Capreolus capreolus italicus*, Maremma wild boar *Sus scrofa majori* (both subspecies endemic to Italy), the native red deer *Cervus elaphus*, Linnaeus (present at Castelporziano since 1889) and two alien species; fallow deer, *Dama dama* and the nilgai, an Asian antelope, *Boselaphus tragocamelus*. The German army occupation in 1943–1944 ravaged the area determining the extinction of nilgai and red deer and a strong decrease of the other species. Hence, two distinct periods can be identified: in the pre-removal period (1878–1941) five ungulate species were present, presumably leading to higher complexity of the inter-specific interactions; during the post-removal period (1950–1986) only three ungulate species were present.

The removal of two of the five species allowed us to study ungulate population dynamics in the same environment for different complexity levels of the ungulate community. There is indeed a long tradition of using accidental removals of one or more species in a community of ungulates as a natural experiment, to test hypotheses about population regulation: Sinclair (1995) used the removal of buffalo *Synacerus caffer* in the northern Serengeti, showing that most species were regulated by predation while Thomson's gazelle *Eudorcas thomsonii* was possibly facilitated by topi *Damaliscus lunatus*. Increasing of ungulate populations following removal of the dominant competitor provide a clue for inter-specific demographic competition, as in the case of the removal of hippopotamus *Hippopotamus amphibius* in Uganda (Eltringham 1974) or the die-off of wildebeest *Connochaetes taurinus* in Kenya (Foster and McLaughlin 1968).

To summarise our work, we performed species-specific GLM analyses (Owen-Smith and Mills 2006) before and after the removal experiment, to test the relative weight of inter- and intra-specific competition as a function of the complexity of the community. The larger is the number of ungulate species, the larger is the potential for inter-specific competition (Putman 1996), associated with increased resource competition owing to lower forage availability for each species, and increased interference competition due to over-crowding. The effects of a lowered complexity on the relative strength of inter- and intra-specific competition is, however, less clear. On one side, intra-specific competition could become relatively stronger for the simpler community of the post-removal period, owing to the reduced number of actors at play. On the other hand, the larger number of animals could reinforce both inter- and intra-specific competition in the more complex community of the pre-removal period. The careful analysis of the population dynamics in the two periods allowed us to select between these two possible responses of the ungulate community.

Using structural equations modelling with latent variables (SEM, Shipley 2000), we tested for the effects of climatic and environmental factors, of the density of potential

competitors and density dependence on the growth rate of wild boar, fallow and roe deer for the whole study period, in order to test the hypothesis that density dependence and competition (regardless specific conditions of the study area) are more relevant than climatic and environmental factors in regulating Mediterranean ungulate populations, in contrast with ungulates living in harsher and more fluctuating environments.

In conclusion, the long time series of population estimates at the Castelporziano Preserve allowed us to test two main hypotheses in the dynamics of this community of Mediterranean ungulates: 1) that the complexity level of the ungulate community affects the strength of intra- and inter-specific competition; and 2) that in the present conditions encountered in Mediterranean environments the effects associated with intra- and inter-specific interactions are stronger than those due to environmental factors such as climate.

## Material and methods

### Study area

The Castelporziano Preserve is a fenced area of 48 km<sup>2</sup> – excluding the area of Capocotta (cf. Focardi et al. 2006) – located a few kilometres southeast of Rome, Italy. In the past, the Preserve was used as a hunting ground by the kings (until World War II) and then by the Presidents of the Italian Republic. This determined the organization of about 10–12 hunting drives per year. In addition to those drives, gamekeepers hunted for supplementary days (0–57) during each hunting season to fulfil shooting plans. After 1976, when sport hunting was forbidden, only harvest by gamekeepers was allowed. No large predators were present in the Preserve through the study and poaching was prevented thanks to careful surveillance by gamekeepers.

More details on the history of the Preserve may be found in Imperio et al. (2010).

### The ungulates

Life history traits of the wild boar at Castelporziano are reported by Focardi et al. (2008). Wild boar is a medium-sized omnivore (at Castelporziano adult females attain 50–70 kg, and adult males 60–90 kg). Most births are observed between late April and late May, indicating that matings take place mainly between December and January. Wild boar females are known to reach sexual maturity even at nine months of age under favourable conditions (Fernandez-Llario and Mateos-Quesada 1998), but the small size of the individuals in the Castelporziano Preserve does not usually allow for such an early development; in this population sexual maturity is reached at 18 months of age. Red deer is a large grazer (adult females weigh about 110 kg, adult males 200 kg), while fallow deer is a medium-sized (50 kg for adult females and 80–90 kg for adult males) generalist herbivore and roe deer is a small browser (18–20 kg) (weights collected at Castelporziano, F. Ronchi and P. Aragno pers. comm.). In cervids, females can breed from their second year; females of fallow and red deer

typically produce only one offspring while roe deer usually two (Hayssen et al. 1993). Mating occurs between September and October in fallow and red deer, and in July–August in roe deer; births were observed between May and June in these three species. The only other ungulate species present in the Preserve (just during the pre-removal period) was the nilgai, a large antelope (170–240 kg) that is both a browser and a grazer (Nowak 1999). No life history data for this species are available for Castelporziano.

### Population density estimates and hunting effort

Population density estimates are obtained from the data base of bag records described by Imperio et al. (2010). Data are available for the period 1878 to 1986 (records are missing in nine out of 109 years, mostly during the two World Wars, thereafter WWI and WWII) and are shown in Fig. 1 (upper panel). Hunting was carried out every year, from November to March of the following year. For short, each hunting season is referred to by using the index *t*, as shown in the lower panel of Fig. 1. Density estimates (*N<sub>t</sub>*) were computed as the number of specimens killed during hunting drives, per km<sup>2</sup> of driven area. The quality of collected data and their validity for the assessment of population density are discussed by Imperio et al. (2010), which showed no relevant bias due to hunting.

For a limited period animals counts are also available (from 1892 to 1942 for wild boars, 1906 to 1942 for all other ungulates; Imperio et al. 2010). Linear correlations between density estimates and animal counts are significant for all the species (roe deer:  $r = 0.86$ ,  $p < 0.0001$ ; fallow deer:  $r = 0.73$ ,  $p < 0.0001$ ; wild boar:  $r = 0.91$ ,  $p < 0.0001$ ; red deer:  $r = 0.38$ ,  $p = 0.03$ ; nilgai:  $r = 0.58$ ,  $p < 0.001$ ). A possible source of bias when using hunting data, is the different spatio-temporal pattern between harvest bag and animal abundance due to local differences in the management of the populations and to a variable hunting pressure between years (Ranta et al. 2008), however the Castelporziano Preserve was a relatively small area with a unique management direction, and we corrected harvest data for hunted area.

Actual harvest rate (HR, number of animals killed/number of animal counted) is available for a limited number of years (1906–1942), for which direct counts of all the species are available. As a proxy for HR, we used a measure of hunting effort (HE, total number of shooting days per hunting season). Shooting plans (based on animal counts) were in fact put into practice by deciding the number of hunting drives to be carried out. It can be shown that  $\log(\text{HE})$  is linearly correlated with HR for all species (fallow deer:  $r = 0.71$ ,  $n = 35$ ,  $p < 0.0001$ ; roe deer:  $r = 0.44$ ,  $n = 35$ ,  $p = 0.009$ ; wild boar:  $r = 0.40$ ,  $n = 49$ ,  $p = 0.005$ ; red deer:  $r = 0.60$ ,  $n = 35$ ,  $p = 0.0001$ ) and hence hunting effort is a reliable proxy for HR.

In most analyses, the total data set was divided in two main periods: the pre-removal period (1878–1942) and the post-removal period (1948–1986). For some analyses, it was also useful to distinguish between pre-removal sub-period A, before WWI (1878–1917), and pre-removal sub-period B, between the WWS (1918–1942). During WWI royal hunts were suppressed (only a few drives were performed by rangers),

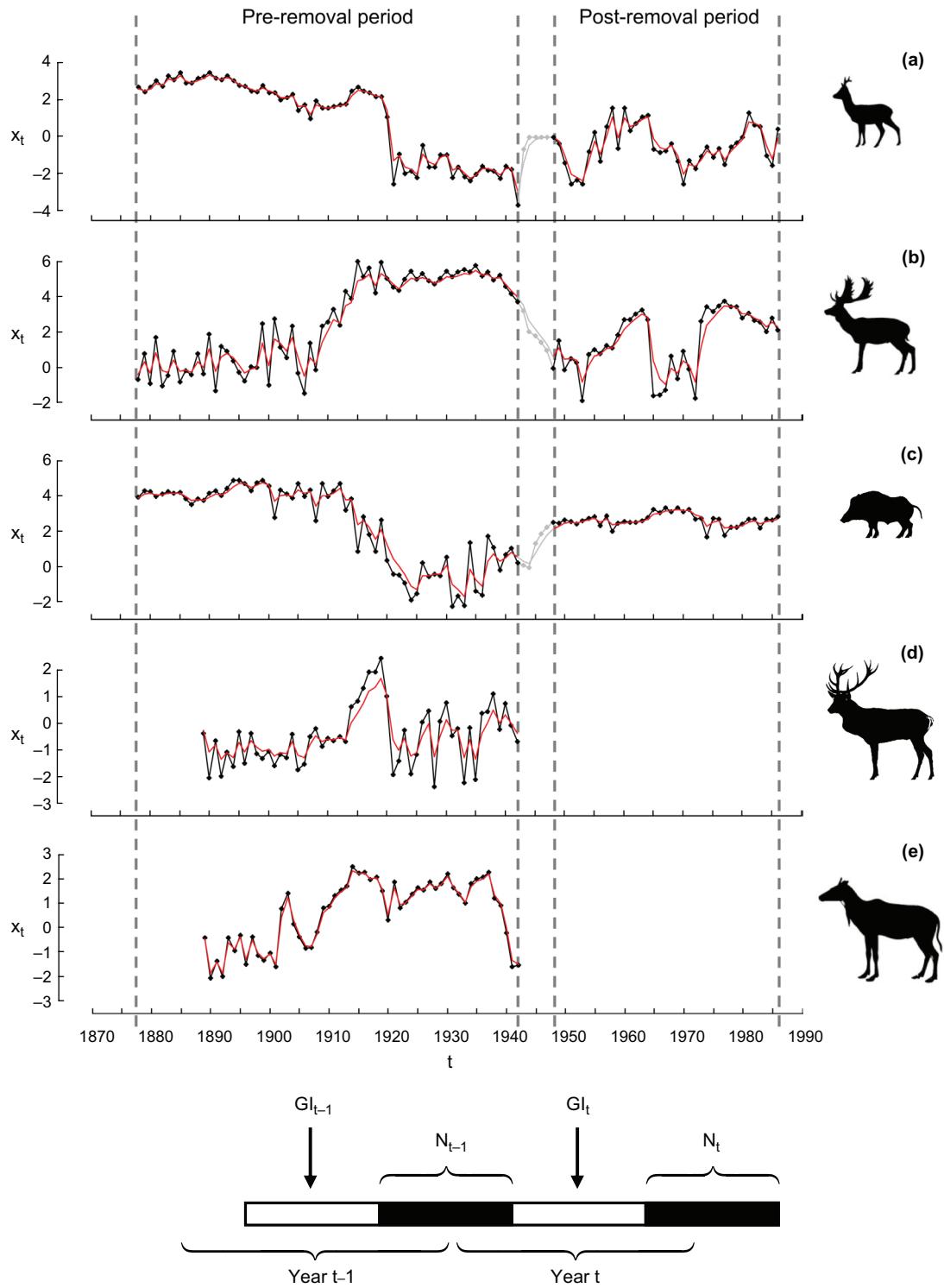


Figure 1. Upper panel: time series of population density estimates from bag data (black lines) for the five ungulate species present in the Castelporziano Preserve from 1878: (a) roe deer, (b) fallow deer, (c) wild boar, (d) red deer, and (e) nilgai; red lines: Kalman-filtered series. The vertical dashed lines indicate the limits of the two periods (pre- and post-removal) considered in the analysis. Lower panel: definition of the variables used in the analysis:  $N_t$  refers to the population density estimate obtained in the fall-winter season between year  $t - 1$  and  $t$ ,  $GI_t$  are the Gaussen indexes for spring-summer in year  $t$ . Hunting seasons (November to March) are represented in black, spring-summer seasons are represented in white.

and immediately afterwards some reforestation took place in the Preserve. These events were followed by a change in ungulate densities: fallow deer reached the highest densities after WWI, while roe deer and wild boar populations declined.

## Climate

The climate is Mediterranean: maximum precipitation occurs in October and November, while summer drought can be severe and prolonged from May to August (CNMCA

2008). To determine climatological conditions, we used the meteorological data recorded by the station of the Collegio Romano in the city of Rome at about 15 km from the Preserve (<[www.romameteo.it/tevere/Collegio%20Romano/collegio\\_romano.htm](http://www.romameteo.it/tevere/Collegio%20Romano/collegio_romano.htm)>). Monthly precipitation and mean temperature data are available for the whole study.

From these data, we computed the GausSEN index (GI, Dajoz 2006) for early spring (March–April,  $GI_{ma}$ ), late spring (May–June,  $GI_{mj}$ ), and summer (July–August,  $GI_{ja}$ ), as the total amount of precipitation (in mm) minus twice the mean temperature (in °C). The GausSEN index is a measure of the water available for vegetation, and can therefore be used as a proxy for resource availability (Toigo et al. 2006). Wet conditions correspond to large GI values, while dry and/or drought conditions correspond to low values. The value of GI during the summer provides information on the severity of summer drought, and thus, indirectly, on the quality and quantity of food available during the harshest season for this type of environment. On the other hand, wet conditions in late spring can affect the survival of newborn piglets or fawns that rest on the ground. Finally, while adult females exhibit low temporal variability in reproduction, the value of GI in spring and summer at time  $t - 1$  can affect the fecundity of young females, contributing to the determination of the population growth rate in the following year. Time series of the GausSEN index in early spring  $GI_{ma}$ , late spring  $GI_{mj}$  and summer  $GI_{ja}$  did not show consistent temporal trends and were highly variable during the study period (mean values ± SDs:  $105.04 \pm 61.41$ ,  $47.19 \pm 53.93$ ,  $-8.39 \pm 38.66$ , respectively). The results of the Pearson correlation test indicate independence between the various GausSEN indices defined above ( $n = 109$ ;  $GI_{ma} - GI_{mj} r = 0.15, p = 0.12$ ;  $GI_{ma} - GI_{ja} r = 0.08, p = 0.43$ ;  $GI_{mj} - GI_{ja} r = 0.02, p = 0.83$ ).

## Vegetation cover

Castelporziano includes one of the most important relict Italian Mediterranean forests (Pignatti et al. 2001). Vegetation consists of natural mixed oak woods with both evergreen (*Quercus ilex* and *Q. suber*) and deciduous (*Q. cerris*, *Q. frainetto*, *Carpinus orientalis*) species, as well as maquis (the typical Mediterranean shrubby vegetation on degraded soils, consisting of densely growing evergreen woody plants less than 5 m tall), especially in the seaward part of the Preserve (Grignetti et al. 1997). At present, a small percentage of land is used for cultivations and pastures. Natural woods were usually exploited until about three decades ago; clear-cuttings were practiced only in case of need of soil tilling, in particular during the 1940s. Later, most of these lands were reforested, mainly with domestic pine *Pinus pinea* or cork oak *Q. suber*.

Reconstruction of past land cover of the Preserve was made possible by the availability of a cadastral map (dated 1867) and of a set of aerial photographs taken in 1930, 1954, 1959, 1969 and 1980 (source: Istituto Geografico Militare, Florence, Italy) and 1943 (source: Royal Air Force, Pigorelli Museum, Rome, Italy), interpreted with the help of a stereoscope (Imperio et al. 2010). The main types of vegetation cover determined from these data are natural woods, open areas and planted stands (mainly domestic pine). We computed the area covered by mixed oak woods and maquis (for

the aims of this paper merged together to form the class of natural woods), and the area covered by pine plantations for each land cover map. The covered area during non-sampled years was obtained by linear interpolation. All geographical data have been elaborated using ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA).

## Population models

The aim of this study is to detect which factors (endogenous and/or exogenous) affect the per capita growth rate  $r$  and thus drive population fluctuations. The discrete growth rate is defined as:

$$r_t = \ln \frac{N_t}{N_{t-1}} = x_t - x_{t-1} \quad (1)$$

where  $r_t$  is the realized per capita rate of change between time  $t - 1$  and  $t$ ,  $N$  is the population density and  $x = \ln(N)$ .

In presence of intra-specific competition for limited resources, or of density-dependent effects (e.g. disease transmission) the growth rate depends on population density. Two of the simplest models for density dependence are the stochastic Gompertz and Ricker models. The Gompertz model has the form:

$$N_t = N_{t-1} \exp(a + b \ln N_{t-1} + \varepsilon_t) \quad (2)$$

while the stochastic Ricker model assumes an exponential density dependence and is written as:

$$N_t = N_{t-1} \exp(a + b N_{t-1} + \varepsilon_t) \quad (3)$$

In both models, a population growth rate is said to be density dependent when  $b$  is negative and significantly different from zero. In all these models, the residuals  $\varepsilon_t$  are assumed to be Gaussian and uncorrelated. For a wider description of population models see Turchin (2003).

## Density dependence tests

To detect density dependence, we performed a least-square-fit of the discrete growth rate  $r_t$  versus the population density estimate on the previous year,  $x_{t-1}$  or  $N_{t-1}$ . To verify whether the regression coefficients were significantly different from zero, we used a shuffling (randomization) method that is a modification of the Pollard test (Jacobson et al. 2004). In particular, we compared the observed test statistic ( $b_{obs}$ ) with the distribution of the  $b_{surr}$  values provided by a large number of surrogate data sets where the correlation between  $r_t$  and  $N_{t-1}$  (or  $x_{t-1}$ ) has been eliminated. In the analysis reported here, the uncorrelated surrogate data are obtained by an ensemble of 10 000 random shufflings of the density values, while the growth rate series remains unchanged. With this choice, any possible cross-correlation between the temporal dynamics of the two signals is destroyed by the random permutation of the elements of one of the two time series. Although theoretically zero, any couple of uncorrelated signals with finite length can however provide by chance a non-null value of the correlation, which is statistically insignificant. From the distribution of  $b_{surr}$ , we can thus estimate the probability of getting by chance a value equal to or larger than the value  $b_{obs}$  (in absolute value sense, i.e. a two-sided test). If this

probability is lower than a chosen threshold (here, 5%), then it is concluded that the value of  $b_{\text{obs}}$  is significantly different from zero. Jacobson et al. (2004) considered several different density dependent tests, concluding that the shuffling technique is more parsimonious than parametric bootstrap since it makes no assumption about the explicit form of the null model.

A jackknife test (Miller 1974) allows for estimating confidence bounds on  $b_{\text{obs}}$  and assessing the influence of outliers. In this test, the observed value  $b_{\text{obs}}$  is compared with the mean,  $\bar{b}_j$ , and the standard deviation,  $\sigma_j$ , of a Jackknife distribution of  $b$  values obtained from 10 000 subsets, each generated by randomly dropping half of data points. The value  $\sigma_b$  provides an estimate of the uncertainty on  $b_{\text{obs}}$ . In addition, the quantity

$$\Delta_b = \frac{\bar{b}_j - b_{\text{obs}}}{\sigma_j} \quad (4)$$

provides information on the relevance of outliers: values of  $|\Delta_b|$  close to one indicate a non-negligible effect of outliers on the parameter value.

The fraction of variance explained by a given model is computed as  $R^2 = \sigma_m^2 / \sigma_r^2$ , where  $\sigma_r^2$  is the variance of the time series of the observed growth rates and  $\sigma_m^2$  is the variance of the deterministic part of the model. Normality of residuals for each model is tested using the Shapiro–Wilk test. If the residuals distribution is not Gaussian, it is likely that some other process driving population fluctuations has been missed.

To compare the strength of density dependence during the two periods for fallow deer, roe deer and wild boar, we performed a t-test between the density-dependence regression slopes ( $b$ ) in the pre-removal and post-removal periods for each species. All density dependence tests have been carried out with the R statistical package (ver. 2.10.1, <[www.r-project.org](http://www.r-project.org)>).

## Data filtering

When population density estimates are potentially affected by significant sampling errors, state-space models (SSM) can be used to filter the original raw data and disentangle sampling error from environmental variability. The proper type of SSM to be adopted depends on the form (if any) of density dependence (De Valpine and Hastings 2002, Staples et al. 2004, Dennis et al. 2006). In the case of density-independence or a Gompertz-like density dependence, the SSM is linear and a Kalman filter approach is appropriate. In the latter case (Gompertz density dependence) the PROC MIXED of SAS 9.2 (SAS Inst.) can be used for estimation (Dennis et al. 2006). We denote

$$y_t = N_t + \eta_t \quad \text{with } \eta_t \in \text{Norm}(0, \sigma_\eta) \quad (5)$$

where  $y_t$  represents the filtered series and  $\eta_t$  the sampling errors. The aim of this analysis is to separate  $\eta_t$  from  $\varepsilon_t$  (Eq. 2).

Since the application of the SSM requires a time series without missing values, the gaps in population density estimates have been filled by appropriate interpolations. In the case of single-year, isolated missing data (five instances in

total), the interpolated values has been obtained as an average between the previous two and the following two years. In case of the critical period 1943–1947, when only data for 1944 were available, we computed the missing data by the linear interpolation between the available data at the two edges of each gap (i.e. interpolation between the 1942 and 1944 values for 1943 and between 1944 and 1948 for the period 1945–1947). Apart from their use in SSM, none of the interpolated data in the period 1943–1947 were used in population dynamics analyses. SSM were estimated using both maximum likelihood and restricted maximum likelihood, as suggested by Dennis et al. (2006), and their results were then compared using AIC values.

## Generalized linear models

We applied generalized linear models (GLM) to the two periods (pre- and post-removal) separately. For each species, we fitted the models using the Kalman-filtered population growth rates as dependent variables and the following set of predictors: 1) natural logarithm of the density of the same species on the previous year,  $t - 1$  (density dependence), 2) density of all the other species at  $t - 1$  (inter-specific interactions), 3) log-transformed hunting effort (lnHE), 4) GI parameters at year  $t$  and  $t - 1$ , 5) amount of natural woods (NW) and 6) amount of pine plantations (PP).

We tested all linear combinations of variables, with the limitation of using a number of variables that did not exceed 15% of the number of available data points (i.e. six parameters for the pre-removal period and five parameters for the post-removal period). The variable 'sub-period' (A/B in the pre-removal period) was included only as an interaction term with the other factors. Other first order interaction terms were considered as biologically relevant: density of one species  $\times$  climatic indices, and density of one species  $\times$  hunting effort, as intra- and inter-specific competition could be exacerbated by unfavourable climatic conditions or stronger hunting pressure. In all multiple regressions, we calculated the t statistic for each term that entered the selected model to assess whether it provided a significant contribution to the model. To select the most appropriate models, we used Akaike's information criterion with finite sample correction (AICc, Burnham and Anderson 2002). Model averaging with Akaike weights was performed following Buckland et al. (1997), including in the computation all the models with evidence ratios (the ratio between the likelihood of the best model and the one of each candidate model)  $> 0.1$ .

Moreover, we carried out the first selected models without the 'density of the same species' factor, and, using the residuals of these models, we calculated the univariate density dependence for fallow deer, roe deer and wild boar in both periods. Again, we performed a t-test between density dependence regression coefficients ( $b$ ) in the pre- and post-removal period for all these three species.

All GLM analyses have been performed with the statistical software SAS 9.2 (SAS Inst.).

## Structural equation modelling

Structural equation modelling (SEM) allows to model networks of causal relationships within a set of explanatory

variables (Shipley 2000, Mysterud et al. 2008). Grace (2007) stresses the usefulness of SEM in wildlife studies: it represents a framework for evaluating and comparing complex hypotheses developed from a theoretical knowledge about the processes responsible for data structure. SEMs are useful because it is possible to deduce latent variables (i.e. variables which cannot be directly estimated in the field) from manifest, measured, correlated variables (similarly to what ecologists do when using the factorial analysis). Relevant, using SEM, it is possible to test causal relationships, accounting for spurious correlations among variables.

First, we developed a theoretical model of the studied guild of ungulates. This was made on the basis of preliminary results – using the GLM analyses as guidelines – and of the theoretical background discussed in the introduction. We did not perform model selection but we evaluated, using a confirmatory approach, to which extent data matched our theory. We used SEM to develop a general model of the community of ungulates through the whole study period. This model is expected to yield a lower level of fit with respect to per-period GLM models, but it may improve the generality of the results and make easier their application to future management challenges in the study area and in similar sites.

The development of a SEM (Shipley 2000) requires the a priori definition of the links among model variables in the form of regression equations:

$$V_1 = \alpha_1 F_1 + \alpha_2 F_2 + \dots + E_{V_1} \quad (6)$$

where  $V_1$  is the dependent variable,  $F_1$ ,  $F_2$ , etc are the independent variables and  $E_{V_1}$  is the error term for  $V_1$ , while the parameters  $\alpha_1$ ,  $\alpha_2$  represent the effects of each independent variable on the dependent variable to be estimated. Given a set of dependent variables  $V_1$ ,  $V_2$ , ..., the aim of the procedure is to minimise the difference between experimental

and predicted variance-covariance matrix. A SEM is constituted by two parts: a structural or causal model describes the relationship between the variables of theoretical interest, while the measurement model describes the relationships between latent variables (the unobserved factors defined by the researcher) and their manifest variables. In our model latent variables were used to represent habitat and climate effects, which were estimated by habitat composition and climatic indexes, while the causal part of the model linked latent variables to density and growth rate of the different species.

In SEM, the traditional distinction between dependent and independent variables is often lost, as a variable which is dependent in one equation can be independent in another one; the relevant distinction becomes that between exogenous variables, which have no causal parents in the model, and endogenous variables which are determined by other model's variables. Here, SEM was used to obtain a strictly confirmatory analysis (with adjustments relative only to the measurement part of the model). We adopted Shipley's (2000) approach to the use of fit indices. The procedure PROC TCALIS (SAS Inst., ver. 9.2) was used for model estimation, using maximum likelihood and a Newton–Raphson optimization technique.

## Results

### Density dependence

The results of the density dependence tests are reported in Table 1 for the four species considered. We performed the analyses on the whole time series spanning the period 1878–1986 (total), on the pre-removal period (1878–1941, except red deer 1890–1941) and on the post-removal period (1950–1986). In all cases but one (roe deer in post-removal

Table 1. Density dependence tests for the four ungulate populations at Castelporziano. From left to right: species; period of study; type of model (Ricker or Gompertz); slope (b) and coefficient of determination ( $R^2$ ) of the density-dependence regression; P: probability value computed from randomization of density values; Jackknife: value of  $\Delta_p$ ; Shapiro–Wilk test: probability value. Significant values ( $p < 0.05$ ) are in bold.

Species	Period	Model	b	$R^2$	P	Jackknife	Shapiro–Wilk test
Fallow deer	<b>total</b>	<b>Gompertz</b>	<b>-0.177</b>	<b>0.08</b>	<b>0.002</b>	<b>0.0198</b>	<b>0.01</b>
	total	Ricker	-0.002	0.01	0.20	0.0492	0.007
	<b>pre-removal</b>	<b>Gompertz</b>	<b>-0.197</b>	<b>0.10</b>	<b>0.01</b>	<b>0.0735</b>	<b>0.10</b>
	pre-removal	Ricker	-0.003	0.03	0.12	0.0289	0.06
	<b>post-removal</b>	<b>Gompertz</b>	<b>-0.242</b>	<b>0.11</b>	<b>0.02</b>	<b>0.0597</b>	<b>0.002</b>
	post-removal	Ricker	-0.017	0.03	0.17	-0.0598	0.006
Roe deer	<b>total</b>	<b>Gompertz</b>	<b>-0.094</b>	<b>0.04</b>	<b>0.03</b>	<b>-0.0042</b>	<b>0.02</b>
	total	Ricker	-0.007	0.004	0.28	0.0117	0.005
	pre-removal	Gompertz	-0.052	0.02	0.19	0.0250	<0.0001
	pre-removal	Ricker	-0.001	<0.001	0.45	-0.0009	<0.0001
	<b>post-removal</b>	<b>Gompertz</b>	<b>-0.459</b>	<b>0.22</b>	<b>0.002</b>	<b>0.0634</b>	<b>0.22</b>
	post-removal	Ricker	-0.446	0.23	0.001	0.0377	0.33
Wild boar	<b>total</b>	<b>Gompertz</b>	<b>-0.142</b>	<b>0.07</b>	<b>0.005</b>	<b>0.0433</b>	<b>&lt;0.0001</b>
	total	Ricker	-0.005	<b>0.04</b>	<b>0.03</b>	<b>-0.0158</b>	<b>&lt;0.0001</b>
	<b>pre-removal</b>	<b>Gompertz</b>	<b>-0.157</b>	<b>0.08</b>	<b>0.02</b>	<b>0.0392</b>	<b>0.58</b>
	pre-removal	Ricker	-0.005	0.03	0.10	-0.0191	0.10
	<b>post-removal</b>	<b>Gompertz</b>	<b>-0.573</b>	<b>0.33</b>	<b>&lt;0.001</b>	<b>0.1024</b>	<b>0.04</b>
	post-removal	Ricker	-0.034	0.25	0.001	-0.0541	0.08
Red deer	<b>pre-removal</b>	<b>Gompertz</b>	<b>-0.720</b>	<b>0.38</b>	<b>&lt;0.0001</b>	<b>-0.0846</b>	<b>0.70</b>
	pre-removal	Ricker	-0.204	<b>0.10</b>	<b>0.02</b>	<b>-0.4619</b>	<b>0.44</b>

Table 2. Maximum likelihood (ML) and restricted maximum likelihood (REML) parameters estimates in the Gompertz state-space model. From left to right: intercept ( $a$ ) and regression coefficient ( $c$ ) of the Gompertz model on the logarithmic scale, variance of real population densities time-series ( $\sigma^2$ ) and variance of the observation error ( $\tau^2$ ). See Dennis et al. (2006) for further explanations of the parameters.

Species	Method	$a$	$c$	$\sigma^2$	$\tau^2$	AIC
Fallow deer	ML	0.11	0.94	0.48	0.67	360.3
	REML	0.07	0.96	0.47	0.67	356.2
Roe deer	ML	0.03	0.94	0.35	0.23	282.8
	REML	0.02	0.97	0.34	0.24	278.9
Wild boar	ML	0.09	0.97	0.18	0.36	279.8
	REML	0.05	0.98	0.17	0.36	275.7
Red deer	ML	-0.14	0.71	0.37	0.48	159.8
	REML	-0.11	0.76	0.35	0.49	158.3
Nilgai	ML	0.03	0.88	0.43	0.08	131.0
	REML	0.01	0.92	0.41	0.09	127.7

period), the Gompertz model accounted for density dependence better than the Ricker model, with a larger percentage of explained variance and values of  $b$  that were, in most cases, significantly different from zero at the 95% level.

The total amount of variance explained by density dependence alone was, however, rather low. For the whole time series, the  $R^2$  values were always lower than 0.08. Larger values were obtained when only one period was considered (pre- or post-removal), with a maximum value for red deer (38%). The absolute value of the Jackknife statistics,  $|\Delta_b|$ , was always lower than 0.1 for the Gompertz model, indicating that the  $b$  parameter was not affected by outliers. On the contrary, the Shapiro–Wilk test was significant for fallow deer, roe deer and wild boar, suggesting a non-Gaussian distribution of residuals. Again, the only exception was red deer for which the residual distribution did not significantly deviate from Gaussian.

The  $b$  value was similar during the two periods for fallow deer ( $t$  test:  $t = 0.31$ ,  $p = 0.75$ ), while it was significantly higher (i.e. less negative) during the first period for roe deer ( $t = 2.55$ ,  $p = 0.01$ ) and wild boar ( $t = 2.62$ ,  $p = 0.01$ ), indicating a stronger density dependence during the post- than the pre-removal period.

We also investigated if population density had a delayed effect on the growth rates, by using modified versions of the Gompertz model (Eq. 2) for different lags from 2 to 10 years. The results indicated the absence of any statistically significant correlation between growth rates  $r_t$  and population densities in years preceding  $t - 1$ .

## Data filtering

The analysis above indicated that the ungulate populations at Castelporziano displayed a significant Gompertz-like density dependence. For this reason, we adopted a linear SSM based on Kalman filter, as described in Dennis et al. (2006). For roe deer, fallow deer and wild boar we assumed that the population was at equilibrium (i.e. the observations started after the population has been fluctuating around carrying capacity for awhile) and the initial population density was treated as an unknown parameter of a stationary distribution. Red deer and nilgai, on the contrary, were assumed to be away from equilibrium as they were introduced in the study area, therefore the known initial population was entered in the model (50 red deer, 12 nilgai). Parameters estimation performed using both maximum likelihood and restricted

maximum likelihood methods is shown in Table 2. Since better results were always obtained with the latter, this was used to fit SSMs for all species. Figure 1 shows the Kalman-filtered series (upper panel, red lines).

## Population dynamics at different complexity levels of the community

Table 3 reports model selection for the pre- and post-removal periods at Castelporziano. All models reported here were significant or nearly significant ( $p < 0.08$ ), and the residuals of most of these models were normally distributed (as shown by the Shapiro–Wilk test), except for roe deer in the pre-removal period and fallow deer and wild boar in the post-removal period. Table 4 shows, for each species, the averaged parameter estimates.

### Roe deer

The most appropriate models for the pre-removal period retained the presence of density dependence and of a significant positive effect of nilgai, and of competition with fallow deer in sub-period B only. There were also indications of a negative effect of pine woods, which were expanding at the end of 19th century, of a positive effect of wetter conditions in early spring (March–April) at year  $t - 1$  and a negative effect of wetter conditions in late spring of the same year ( $t$ ). In the post-removal period, density dependence was always present. The presence of wild boar (with negative effect) emerged as a possible, but non-significant, element.

### Fallow deer

In the pre-removal period, density dependence (always significant) and a positive effect of pinewood (significant in some of the models) were detected. Some models also included the (non-significant) negative effects of wild boar density and of wetter conditions in May–June of year  $t$ . Again, the presence of nilgai emerged as a positive effect. In the post-removal period, density dependence was significant, together with the negative effect of hunting and a strong positive effect of wetter conditions in spring/summer of the previous year ( $t - 1$ ).

### Red deer

In addition to density dependence, always present, the population growth of this species appeared to be influenced by a form of facilitation by roe deer and nilgai, by a strong positive effect of pine wood and a negative effect

Table 3. Selection of the population models for the four ungulate species at Castelporziano. The five models with the lowest AICc are listed for each species and for the pre- and post-removal periods separately. The AICc values, Evidence ratios (ER) and probability values of Shapiro-Wilk test for residuals are reported in the last three columns. The variables are  $x_{t-1}$ (species): log-transformed density of the species at time  $t-1$ ;  $Gl\_ma$ ,  $Gl\_mj$ ,  $Gl\_ja$ : Gaussen indices in early spring, late spring, and summer, respectively, at time  $t$  and  $t-1$ ;  $InHE$ : log-transformed hunting effort;  $NW$ : natural woods;  $PP$ : pine plantations;  $per$ : sub-periods (A or B) of the pre-removal period. Asterisk indicate interaction between two variables. The sign of the parameter estimate is indicated in square brackets for each factor with significance at least at the  $p \leq 0.15$  level. All significant factors at the  $p \leq 0.05$  level are in bold.

Species	Models	AICc	ER	Shapiro-Wilk test
Roe deer	Pre-removal period			
	$x_{t-1}(roe\ d.) [-]; x_{t-1}(nilgai) [+]; PP*per [-,-]$	66.3	1.00	0.003
	$x_{t-1}(roe\ d.) [-]; x_{t-1}(\text{fallow d.})^*per [0,-]; x_{t-1}(nilgai) [+]; PP*per [-,0]$	68.1	0.40	0.02
	$x_{t-1}(roe\ d.) [-]; x_{t-1}(nilgai) [+]; PP*per [-,-]; Gl\_ma_{t-1} [+]$	75.7	0.01	0.004
	$x_{t-1}(roe\ d.) [-]; x_{t-1}(nilgai) [+]; PP*per [-,-]; Gl\_mj_t [-]$	76.1	0.01	0.02
	$x_{t-1}(roe\ d.) [-]; x_{t-1}(\text{fallow d.})^*per [0,-]; x_{t-1}(nilgai) [+]; PP [-]; Gl\_ma_t [-]$	76.6	0.01	0.13
	Post-removal period			
	$x_{t-1}(roe\ d.) [-]; x_{t-1}(\text{wild b.}) [-]; NW$	78.9	1.00	0.22
	$x_{t-1}(roe\ d.) [-]; x_{t-1}(\text{wild b.}) [-]; NW; PP$	80.4	0.45	0.21
	$x_{t-1}(roe\ d.) [-]$	81.2	0.31	0.24
Fallow deer	$x_{t-1}(roe\ d.) [-]; x_{t-1}(\text{fallow d.})$	82.5	0.16	0.32
	$x_{t-1}(roe\ d.) [-]; x_{t-1}(\text{wild b.}); NW; Gl\_mj_{t-1} [+]$	87.0	0.02	0.42
	Pre-removal period			
	$x_{t-1}(\text{fallow d.}) [-]; x_{t-1}(nilgai) [+]; PP [+]$	99.9	1.00	0.44
	$x_{t-1}(\text{fallow d.}) [-]; x_{t-1}(\text{wild b.}); x_{t-1}(nilgai) [+]; PP$	102.1	0.33	0.71
	$x_{t-1}(\text{fallow d.}) [-]; PP [+]$	106.4	0.04	0.60
	$x_{t-1}(\text{fallow d.}) [-]; x_{t-1}(nilgai) [+]; PP [+]; Gl\_mj_t [-]$	107.5	0.02	0.71
	$x_{t-1}(\text{fallow d.}) [-]; x_{t-1}(roe\ d.) [+]; x_{t-1}(\text{wild b.}) [-]; x_{t-1}(nilgai) [+]; PP [+]; Gl\_mj_t [-]$	108.1	0.01	0.51
	Post-removal period			
	$x_{t-1}(\text{fallow d.}) [-]; Gl\_ma_{t-1} [+]; InHE [-]$	91.7	1.00	0.04
Red deer	$x_{t-1}(\text{fallow d.}) [-]; Gl\_ma_{t-1} [+]; Gl\_mj_{t-1} [+]; NW [+]; InHE [-]$	95.7	0.14	0.23
	$x_{t-1}(\text{fallow d.}) [-]; Gl\_ma_{t-1} [+]; Gl\_mj_{t-1} [+]; InHE [-]$	97.6	0.05	0.005
	$x_{t-1}(\text{fallow d.}) [-]; Gl\_ma_{t-1} [+]; Gl\_ja_{t-1} [+]$	98.3	0.03	0.02
	$x_{t-1}(\text{fallow d.}) [-]; Gl\_ma_{t-1} [+]; Gl\_ja_{t-1} * x_{t-1}(\text{wild b.}) [+]; InHE [-]$	99.3	0.02	0.004
	Pre-removal period			
Wild boar	$x_{t-1}(\text{red d.}) [-]; x_{t-1}(roe\ d.) [+]; x_{t-1}(nilgai) [+]; NW [-]; PP [+]$	70.7	1.00	0.24
	$x_{t-1}(\text{red d.}) [-]; x_{t-1}(roe\ d.) [+]; PP [+]$	71.7	0.60	0.06
	$x_{t-1}(\text{red d.}) [-]; x_{t-1}(roe\ d.) [+]; NW [-]; PP [+]$	71.8	0.59	0.21
	$x_{t-1}(\text{red d.}) [-]; x_{t-1}(roe\ d.) [+]; x_{t-1}(nilgai) [+]; NW [-]; PP [+]; Gl\_mj_t [-]$	78.8	0.02	0.46
	$x_{t-1}(\text{red d.}) [-]; x_{t-1}(roe\ d.) [+]; NW [-]; PP [+]; Gl\_mj_t [-]$	80.6	0.01	0.31
Wild boar	Pre-removal period			
	$x_{t-1}(\text{wild b.}) [-]; x_{t-1}(roe\ d.)^*per [0, +]; x_{t-1}(\text{red d.})^*per [-,0]; NW^*per [-,-]$	84.2	1.00	0.37
	$x_{t-1}(\text{wild b.})^*per [-,-]; x_{t-1}(roe\ d.)^*per [-,+]; NW^*per [-,-]$	86.1	0.84	0.17
	$x_{t-1}(\text{wild b.})^*per [0,-]; NW [-]$	87.4	0.20	0.90
	$x_{t-1}(\text{wild b.}) [-]; x_{t-1}(\text{red d.})^*per [-,0]; NW^*per [-,-]$	89.4	0.07	0.85
	$x_{t-1}(\text{wild b.})^*per [-,-]; x_{t-1}(\text{red d.})^*per [-,0]; NW^*per [-,-]$	90.1	0.05	0.87
	Post-removal period			
	$x_{t-1}(\text{wild b.}) [-]; InHE [+]$	-18.9	1.00	0.19
	$x_{t-1}(\text{wild b.}) [-]; InHE [+]; NW$	-18.1	0.69	0.63
	$x_{t-1}(\text{wild b.}) [-]$	-16.8	0.35	0.002
	$x_{t-1}(\text{wild b.}) [-]; NW$	-15.6	0.20	0.002
	$x_{t-1}(\text{wild b.}) [-]; InHE [+]; NW[-]; PP$	-14.3	0.10	0.35

of woods. As for other cervids, May-June wet conditions at time  $t$  showed a negative effect on the population growth rate.

#### Wild boar

In the pre-removal period, this species appeared to be controlled by density dependence, while increasing woods in the Preserve resulted unfavourable. Roe deer affected positively wild boar, while red deer had a negative effect on this species.

The post-removal period was characterised by density dependence and an apparent positive effect of hunting.

The residuals of the modified selected models (with all selected factors but density of the same species) were used to compute new density-dependence regressions. Again, the regression coefficients were always lower during the second period (roe deer  $t$  test:  $t = -2.34$ ,  $p = 0.02$ ; wild boar  $t = -2.10$ ,  $p = 0.04$ ), but not significantly for fallow deer ( $t = -1.41$ ,  $p = 0.16$ ).

Table 4. Model averaging for the population growth rates of the four ungulate species at Castelporziano. For each species, the averaged parameter estimates of all variables included in the models with evidence ratio  $\geq 0.1$  are weighed with the corresponding Akaike weight, according to the equation 1 of Buckland et al. (1997). Standard deviations are computed following Eq. 9 of the same article. Probability values (p) refers to test Z for the difference of each parameter estimate from zero.

Species	Variable	Pre-removal period		Post-removal period	
		Parameter estimate	p	Parameter estimate	p
Roe deer	Intercept	$2.33 \pm 0.52$	<0.0001	Intercept	$11.39 \pm 13.53$
	$x_{t-1}$ (roe d.)	$-0.44 \pm 0.09$	<0.0001	$x_{t-1}$ (roe d.)	$-0.31 \pm 0.12$
	$x_{t-1}$ (fallow d.)*per	$-0.10 \pm 0.14$	0.09	$x_{t-1}$ (fallow d.)	$0.01 \pm 0.01$
	$x_{t-1}$ (nilgai)	$0.30 \pm 0.09$	<0.0001	$x_{t-1}$ (wild b.)	$-0.67 \pm 0.46$
	PP*per	$-2.51 \pm 2.62$	0.01	NW	$-0.37 \pm 0.36$
Fallow deer	Intercept	$0.14 \pm 0.45$	0.16	Intercept	$-0.92 \pm 3.83$
	$x_{t-1}$ (fallow d.)	$-0.38 \pm 0.03$	<0.0001	$x_{t-1}$ (fallow d.)	$-0.18 \pm 0.09$
	$x_{t-1}$ (wild b.)	$-0.02 \pm 0.03$	0.11	GL_ma <sub>t-1</sub>	$0.003 \pm 0.002$
	$x_{t-1}$ (nilgai)	$0.33 \pm 0.10$	<0.0001	GL_mj <sub>t-1</sub>	$0.001 \pm 0.001$
	PP	$0.56 \pm 0.33$	0.004	InHE	$-0.35 \pm 0.20$
Red deer	Intercept	$0.79 \pm 3.60$	0.18	NW	$0.07 \pm 0.08$
	$x_{t-1}$ (red d.)	$-0.83 \pm 0.14$	<0.0001		
	$x_{t-1}$ (roe d.)	$0.50 \pm 0.12$	<0.0001		
	$x_{t-1}$ (nilgai)	$0.08 \pm 0.06$	0.04		
	NW	$-0.15 \pm 0.08$	0.002		
Wild boar	Intercept	$16.97 \pm 4.80$	<0.0001	Intercept	$1.94 \pm 2.74$
	$x_{t-1}$ (wild b.)	$-0.37 \pm 0.20$	0.02	$x_{t-1}$ (wild b.)	$-0.23 \pm 0.12$
	$x_{t-1}$ (wild b.)*per	$-0.59 \pm 0.37$	<0.001	InHE	$0.09 \pm 0.04$
	$x_{t-1}$ (roe d.)*per	$0.15 \pm 0.78$	0.17	NW	$-0.06 \pm 0.05$
	$x_{t-1}$ (red d.)*per	$-0.36 \pm 0.26$	0.01		
	PP	$-0.02 \pm 0.02$	0.07		
	PP*per	$-0.97 \pm 0.81$	0.004		

### Intra- and inter-specific interactions versus environmental control

The graph of the estimated model is reproduced in Fig. 2, which reports also the parameter estimates. Note that the SEM model did not account for the presence of red deer which, as shown by the species-specific analyses above, had scarce direct and indirect links with the other species. The measurement part of the model (Fig. 2a) allowed us to evaluate three latent variables, habitat quality, climate of year t and climate of year  $t - 1$ . We found that climatic variables were well represented by the respective GausSEN indexes computed for March–April, May–June and July–August. Note that the GausSEN index for July–August was less significant than in other periods. Habitat quality was a construct which depended on both habitat composition and rainfall. Thus the effect of climate could be both direct and indirect, through modification of vegetal productivity. The structural or causal part of the model is displayed in Fig. 2b. According to GLM results we have introduced paths between climate variables and habitat quality only for the growth rates of roe and fallow deer. Intra-specific competition was likely to have an important role for all three species, while the effect of inter-specific competition is represented by coefficients  $\alpha_2$ ,  $\beta_2$ ,  $\gamma_2$ ,  $\gamma_3$ .

The fit of this model was not particularly good as shown by the value of the unbiased CFI estimator (0.59), the ratio  $\chi^2 / DF$  (4.2) and the RMSEA value (0.18, CI = 0.16–0.20). Fit problems were also revealed by the large CV of some parameters (Fig. 2) particularly in the structural part of the model ( $\alpha_3$ ,  $\alpha_4$ ,  $\beta_3$ ,  $\beta_4$ ). The distribution of residuals (Fig. 3)

was well clustered around zero and there were very few residuals beyond  $\pm 2$  standard deviations; in addition, several parameters (such as  $\alpha_1$ ,  $\alpha_2$ ,  $\beta_1$ ,  $\beta_2$ ) were estimated with precision. The larger residuals were relative to the relationships between natural wood and fallow deer density (6.2), natural wood and wild boar (−4.2), and the effect of pine wood on the growth rate of roe deer (−4.2). In general, the parameter values with lower precision were those associated with paths referring to habitat quality. The theoretical expectations that the growth rates were depending on both habitat and climate conditions as well on biotic interactions, were not completely supported by data. Indeed by eliminating all effects from habitat and climate there was a small improvement of fit ( $\Delta AIC = 2.8$ ). Of course, we cannot exclude that different definitions of the variable ‘habitat quality’ could modify the results.

As expected, path coefficients of the measurement part of the model were quite significant, with the exception of variable  $GI_{ja}$  which, on average, appeared not very relevant. However this variable was characterised by a very large CV indicating a strong between-year variability, probably due to the presence of few extreme drought events in summer.

The plot of Fig. 2b illustrates how both intra- and inter-specific competitions had a stronger effect than habitat and climate on the growth rates of the three studied species. Although these populations were mainly regulated by density dependence, also inter-specific relationships appeared to play an important role, especially for roe deer which suffered fallow deer competition ( $\alpha_2$ ). There were reciprocal negative path coefficients between fallow deer and wild boar which

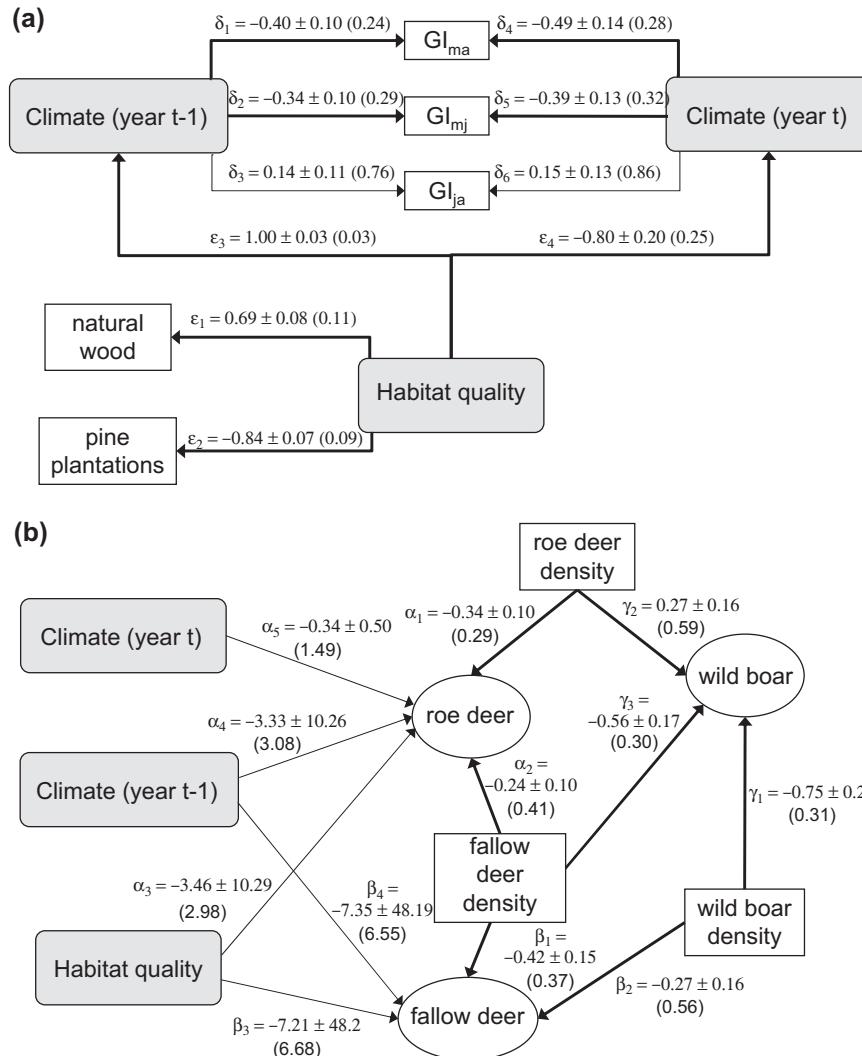


Figure 2. Structural model for the community of ungulates in the Preserve of Castelporziano (Italy) in the period 1878–1986. (a) measurement part and (b) structural part of the model. Grey boxes represent latent variables: climate of the current year, climate of previous year and habitat quality. Climatic latent variables are identified by 3 Gaussen indexes (for early spring  $GI_{ma}$ , fawning period  $GI_{mj}$  and summer  $GI_{ja}$ ) while habitat quality is identified by the proportion of natural and pine wood and by climatic latent variables. Ovals represent the endogenous variables (population growth rates,  $r_i$ ) to be predicted and squared boxes represent the estimated exogenous variables. Bold arrows indicate regression parameters significantly different from 0 ( $p \leq 0.05$ ). For each path, parameter estimate  $\pm$  standard error (coefficient of variation) are shown.

appeared to be stronger on the wild boar. A weak effect of facilitation of roe deer on wild boar was found. Environmental conditions weakly influenced the two cervids, but not the wild boar. By introducing paths to wild boar growth rate from habitat quality, climate (t) and climate (t – 1), no relevant improvement on the fit was found ( $\Delta AIC = 0.1$ , 1.5, –0.4, respectively).

## Discussion

To our knowledge, this paper presented the first long-term analysis of the population dynamics of a community of ungulates living in a Mediterranean climate. Data validation (Imperio et al. 2010) indicated that the effects described in this paper were ecological and did not depend on the hunting regime carried out in the Preserve.

We investigated the role of intra- and inter-specific competition on the dynamics of four ungulate species, together with the effects of both environmental and climatic factors. In particular, the presence of an accidental removal experiment during WWII allowed us to study this ungulate community for different numbers of component species. The main hypotheses tested in this work were that 1) the complexity of the ungulate community influences the relative strengths of intra- and inter-specific interactions (explored by GLM approaches); and 2) in Mediterranean ungulate communities, exposed to relatively mild climate fluctuations, trophic interactions such as density dependence, competition and facilitation have stronger effects than environmental controls such as climate (explored by a SEM approach).

The results of all analyses indicated that intra-specific competition was a main ingredient in the regulation of the growth rates within the ungulate community at Castelporziano,

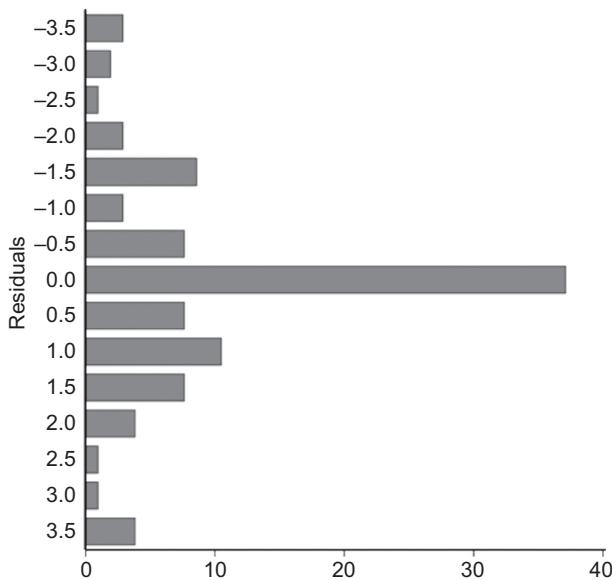


Figure 3. Distribution of residuals for the structural equation model shown in Fig. 2.

in keeping with the view that density-independent regulation is more important in those populations facing strong climatic fluctuations (Post 2005). Both period-specific GLM analyses and SEM indicated the presence of a strong density dependence in the studied species. This effect was indeed larger during the post-removal period, presumably owing to a reduction of between-species interactions (fewer species, lower densities) during this period. The strong impact of WWII on the study area, when the two largest ungulate species were completely extirpated, led to a considerably different composition of the ungulate community, with evident cascade effects on the dynamics of the various species. Ungulate species left in the Preserve, with a lower number of competing species, were thus mainly regulated by density dependence after the removal.

Inter-specific competition, on the contrary, appeared to be generally of lower importance, although evidences of interactions among species were found. Perhaps the most relevant impact was that of fallow deer on the dynamics of roe deer, which, however, was only evident during pre-removal sub-period B, presumably as a consequence of the very high fallow deer density at that time. Results of the SEM model suggest that the observed inverse correlation between fallow and roe deer densities was not a side effect of spurious correlations with unknown variables but, instead, was due to a direct competition between the two species (Putman 1996). This finding is consistent with the available information on inter-specific competition in Mediterranean environments (Focardi et al. 2006, Ferretti et al. 2008).

Other effects included the negative influence of wild boar on fallow deer, the negative effect of red deer on wild boar, and the apparent positive effect of roe deer on red deer and wild boar. The interpretation of these latter effects is however less straightforward. Results of this study suggest that the negative effect of wild boar on fallow deer was probably indirect, related to the impact of selection hunting to control wild boar. The higher the wild boar density, the more intense

presumably was the hunting pressure, with a larger number of hunting drives affecting also other ungulates such as fallow deer. On the contrary, the apparent facilitation exerted by roe deer could be caused by a spurious correlation with a third unknown variable. A pattern of positive correlation between wild boar and roe deer was also observed by Mysterud et al. (2007) in Poland, but it appears theoretically difficult to imagine which mechanisms were operating. A possible explanation is that both species were positively influenced by acorn production: since the two species are polytocous, they could be in the best biological conditions to exploit the window of opportunity represented by masting.

The Lotka–Volterra modeling approach (cf. Tilman 2007) suggests that a stable equilibrium among competing species should be attained, whether inter-specific competition is weaker than intra-specific competition. In our study area this appears true for the pre-removal period. The negative impact of large populations in competition seems to have been counterbalanced by nilgai which facilitated the three species of cervids. A possible mechanism is represented by diet apportionment between nilgai and the other species. Theoretical modelling shows that under some circumstances, large grazers can facilitate food availability for smaller species by stimulating short regrowths of grazed plant species (Illius and Gordon 1987, Farnsworth et al. 2002), as also shown for cattle and red deer by Kuiters et al. (2005). Although this seems to be the more plausible mechanism, other alternative hypotheses cannot be ruled out: for example, nilgai could selectively consume plant species, not directly used by other species, hence a positive effect of nilgai abundance would be expected on the growth rate of other ungulates. This hypothesis is supported by the findings of Solanki and Naik (1998), who calculated a higher proportion of forbs in the nilgai diet with respect to other wild herbivores (which prefer grasses or legumes) and a more diversified feeding habit. After WWII, the concomitant extinction of the largest herbivores and an active policy of tree plantations may have determined an overall reduction of forage availability (especially grasses and browse). Indeed, Imperio et al. (2010) demonstrated a 30% reduction in the surface covered by open areas at Castelporziano, between pre- and post-removal periods.

The hunting effort did not seem to play an important role in determining the growth rate of any of these species, except for fallow deer in the post-removal period. Habitat composition and climate have been shown to affect to some degree the four species. However, these effects had a secondary importance with respect to intra- and inter-specific competition in regulating the ungulate populations studied here. Habitat factors entered the models either in terms of the extent of different habitat types (pine woods vs mixed oak woods in GLM analysis) or as the latent variable ‘habitat quality’ in the SEM model. Unfortunately, no information on actual resource availability (e.g. mast production) was available.

As for the climate, very wet conditions in May–June appeared to play a negative role for all deer species, probably being associated with insurgence of thermoregulatory problems in fawns (Van Moorter et al. 2009). On the contrary, water availability during the spring of the previous year had a positive effect on both fallow and roe deer. This effect is presumably due to increased primary productivity during

moist springs, which in turn improves body conditions in young females and thus enhances their fecundity (Gaillard et al. 1992). Neither of these factors, however, had any effect on wild boar dynamics. This result is consistent with observations on modern data, showing a weak effect of climate on this species and mainly on subadult males (Focardi et al. 2008). Finally, summer drought has been shown to play an almost insignificant role in the dynamics of the studied species. In general the summer Gaussen index values fluctuated widely during the entire span of the study period but no clear downward trend was observed. However, our data set ends in 1986, whereas the mean annual temperature started to grow more rapidly afterwards (Brunetti et al. 2006). The importance of climatic factors, and in particular of summer droughts, could thus grow in coming years, as climate change projections indicate an expected increase of aridity and of heat waves in most Mediterranean regions (Gao and Giorgi 2008).

The results of this study provided also important information on the population dynamics of individual species. Fallow deer appeared not to be much influenced by the other herbivores. This independence is presumably linked to its trophic position (between intermediate and roughage eaters) in the community of ungulates (Hofmann 1989), as fallow deer is able to exploit low quality browse but also to benefit from the flushing of grasses during some periods of the year. This opportunistic foraging habit may have allowed this species to reach impressive densities such as those recorded between the two WWs. For this species, the final regulatory mechanism was represented by a combination of climatic factors and density dependence, together with a positive effect of the amount of pine plantations.

Red and roe deer represent two opposite cases of population regulation. On one hand, direct density dependence was the main controlling factor of the red deer population at Castelporziano, together with vegetation composition. Direct density-dependence explained the growth rate of roe deer at a much lower extent, being influenced by habitat factors (in particular by a negative impact of pine woods), climate and competition with fallow deer. These observations are consistent with life history theory of ungulates. Red deer are capital breeders which are much less susceptible than roe deer to vagaries of climate. Species with a large body size presents a more efficient ruminating system, especially for roughage feeds, and are characterised by larger potential niche than small species and, finally, are dominant in interference. The dominant competitor was thus intra-specifically regulated, while roe deer appeared to be regulated more by external factors. Density dependence in roe deer is well established even in south-European populations (Focardi et al. 2002, Kjellander et al. 2006), but in previous study cases roe deer had no competitors. At Castelporziano, density dependence was operating but it was accompanied by other relevant regulatory processes.

The wild boar population appeared to be scarcely linked to the other ungulates. Theoretical considerations (Focardi et al. 2008) suggest in fact that the demography of this suid is quite different from that of the other species.

This study was made possible by the availability of an exceptionally long data set: because of the peculiar management model of Castelporziano, bag records and other types

of information were carefully conserved for more than one century. This allowed for estimating harvest density (Imperio et al. 2010); in addition, climate records and the availability of unusually-old aerial photographs allowed to carefully track habitat variations in the area. We have to note that an important drawback of the data analyzed here was the lack of information on population structure. In addition, the data were characterized by a high level of noise and by several years during which population sampling was poor, a problem that was addressed by the use of a SSM to filter the data prior to the GLM and SEM analyses. The results presented here should be used to formulate working hypotheses to be verified with recent data, collected in a more controlled way, in order to disentangle the role of competition and climatic control on sex and age-specific vital rates of the populations.

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