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ORIGINAL ARTICLE

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Abstract Detecting density-dependence (DD) in population fluctuations is essential for population control, herd management and harvest programs. However, little information has been obtained for deer in Mediterranean ecosystems. We assess the effects of density, climate and harvesting on population growth fluctuations of two sympatric red (*Cervus elaphus hispanicus*) and fallow deer (*Dama dama*), in two hunting reserves located in a protected area of south-east Spain. We use time series analysis of 16 consecutive years of abundance estimates and hunting extractions. We hypothesized a negative influence of density, deer hunting and drought on population growth rates. Through an integrative Bayesian state-space modeling making possible a unified population analysis we have been able to not only estimate the effects of DD, climate and harvest extractions but also to evaluate their relative impacts on deer population in each location. We found deer populations exhibiting a very strong potential to grow from low density. We detected DD having a stronger effect than hunting and climatic factors, especially for overabundant deer populations close to their carrying capacity. Density-dependent mechanisms compensate harvest extractions, reducing hunting effectiveness. Severe summer drought conditions had negative effects on growth rates and eventually led to delayed autumn deer deaths. The weather effect is more important the more abundant the deer are. In a climate change context, in Mediterranean environments the importance of weather factors could become much greater if both ungulates' densities and aridity increase. Population size control here could modulate the negative effects of climatic constraints on deer and ecosystems conservation.

Keywords Deer population dynamics · Density-dependence detection · Climatic constraints · Management culls · Mediterranean ecosystems conservation

Introduction

The increases of herbivore pressure associated with high density occur on a global scale, having strong impacts on natural ecosystems and inflicting economic losses on forestry and agriculture (Côté et al. 2004; Nugent et al. 2011). In the absence of natural predators hunting becomes the main tool of wildlife managers in deer population control, and the mortality caused by intensive hunting can be the dominant demographic factor affecting deer populations (Solberg et al. 1999; Bender et al. 2004). However hunting is not always efficient in reducing population size (Putman et al. 2005; Nugent et al. 2011; Simard et al. 2013). Many studies have shown that density-dependence, which works as a self-regulatory mechanism, affects recruitment rates and population growth in large mammals (Clutton-Brock et al. 1987; McCullough 1999; Bonenfant et al. 2009). In density-dependent populations, mortality decreases or births increase as population density decreases and vice versa. Moreover, population variations may also be the results of fluctuations in the environment from one time step to the next (Berryman and Turchin 2001). Many environmental stress sources including climatic ones are called density-independent factors, as they affect population growth irrespective of the density. The complexity of interactions between density-dependence and climate (Coulson et al. 2001; Hixon et al. 2002) as well as the wildlife managers' impact on population through hunting extractions make the distinction difficult between intrinsic and extrinsic factors affecting the population.

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The utility of incorporating elasticity analyses into state-space population models, and the need to include climatic processes in planning and wildlife management policies have been highlighted (Koons et al. 2015). However, probably because of the complexity of detecting density-dependent processes, harvest management according to logistic theory is rare for ungulates and upland game (Guthery and Shaw 2013). Few empirical studies have quantified density effects on population growth rates while considering hunting pressure and climatic effects (i.e. Patterson and Power 2002), and very little information has been obtained for deer in Mediterranean ecosystems (Focardi et al. 2002; Rodríguez-Hidalgo et al. 2010; Imperio et al. 2011) where the hardest season is the hot dry summer instead of the cold winter of northern environments (Aanes et al. 2000; Simard et al. 2012).

In the European Mediterranean biogeographical region, and specifically the Eastern part of the Sierra Morena mountains in Southern Spain, there is an important ecosystem housing stable populations of several emblematic protected species coinciding with important game populations. In this area, a *Special Area of Conservation* of the Natura 2000 network, hunting is an old tradition and today is the main economic activity above agriculture and stockbreeding. Here there is an example of overabundant hunting populations in part because the hunting management model from the 1970's on has been characterized by the use of game fences to surround estate perimeters, supplementary feeding and high population densities. In the case of the red deer (*Cervus elaphus hispanicus*), the most abundant game, an average of over 9000 deer have been hunted annually in this area of around 2000 km^2, reaching even higher hunting levels in years of strong drought, with populations probably above carrying capacity (Azorit 2005). Fallow deer (*Dama dama*) density has increased considerably since the 1950's, when they were introduced into some game reserves from which they have been spreading. With a residual population of wolves (Muñoz-Cobo et al. 2000) hunting becomes the main tool of wildlife managers for the control of ungulate populations in an overabundant situation in ecologically valuable protected areas. In this context evaluating the relative importance of all ecological drivers responsible for free-living deer population fluctuations is challenging not only for management but for conservationists as well.

This manuscript reports for the first time an original analysis of yearly variations in population size and assesses the effects of density, climate and harvesting on population growth fluctuations of two deer species living in sympatry in Mediterranean ecosystems, red (*Cervus elaphus hispanicus*) and fallow (*Dama dama*) deer. We use a time series analysis of 16 consecutive years of estimates of abundance and hunting extraction records in two enclosed hunting official reserves located separately in the Sierra Morena Mountains of Jaén, south-east Spain. We explored direct density-dependence (DD) on annual population growth using a version of the Bayesian state-space model (Koons et al. 2015). Bayesian state-space modeling makes possible a unified population analysis including the latent process of population dynamics and the observation process (Iijima and Ueno 2016). Since these models allow us to consider the hunting process implicitly, a more reliable detection of DD can be obtained.

We hypothesized a negative influence of density, deer hunting and drought on population growth rates. Because the red deer populations in this area have been recorded in an overabundant situation, close to or even above their ecological carrying capacity over the last decades (Azorit 2005), we expect the detection of density dependence in both reserves. Meanwhile, for the fallow deer we do not expect DD detection in SC because this species is only just present since the late eighties in this reserve and with a low density. Studying sympatric red and fallow deer in two separate populations allows us a better assessment of the effects of density and hunting pressure in the same climatic regime. Due to a higher aridity in summer we expected the strong effects of climatic conditions to modulate the DD strength similarly to those reported in northern populations (Aanes et al. 2000). But the negative effect of climatic constraints is expected to occur at the end of summer because of the lack of rainfall rather than in winter due to snow as in northern environments. Our findings may provide new and useful information for the management of deer populations in semiarid Mediterranean environments facing climate change.

Materials and methods

Study Area

The study was conducted in Lugar Nuevo (LN) and Selladores-Contadero (SC), two enclosed official estates of 100 km^2 each. They are located separately in the Sierra de Andújar Natural Park in the Sierra Morena Mountains of Jaén, south-east Spain (38°9′N; 4°3′W and 38°23′N; 3°47′W respectively, Fig. 1). These protected areas host emblematic endangered species such as the Iberian lynx (*Lynx pardina*). At the same time they have been important traditional game reserves, hunting being the main economic resource in this area. Red deer (*Cervus elaphus hispanicus*) is the most abundant and important game in both reserves. Fallow deer (*Dama dama*) density has increased since the nineteen-fifties in LN, and since the late eighties in SC. At the same time the game ungulate species living in this area include wild boar (*Sus scrofa*), mouflon (*Ovis aries musimon*) and Iberian ibex (*Capra pyrenaica*). The presence of predators such as the wolf (*Canis lupus signatus*) is increasingly scarce in these areas (Muñoz-Cobo et al. 2000).

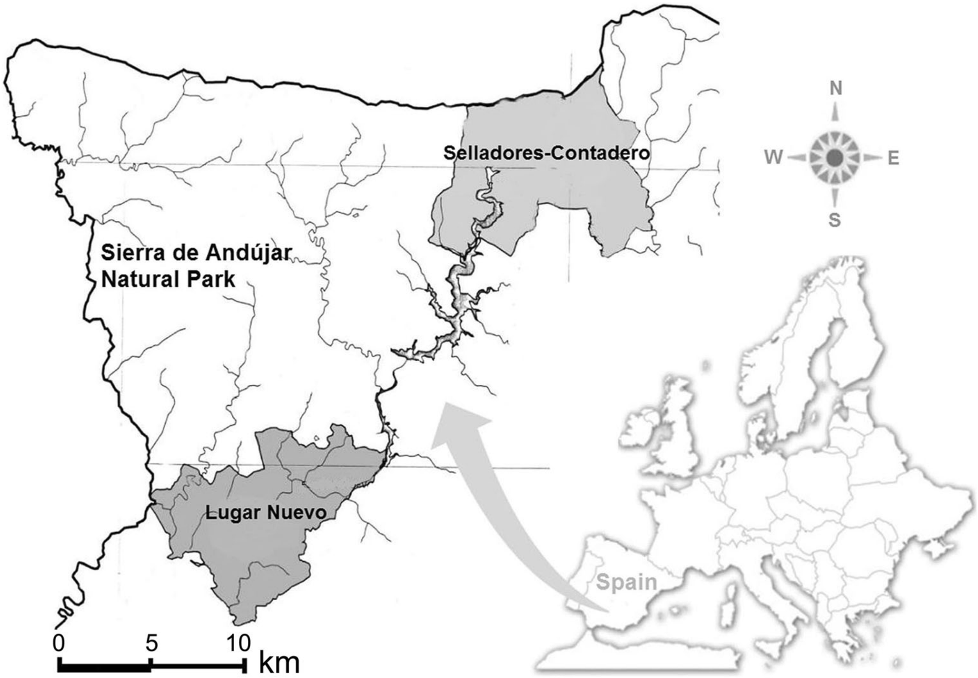

Fig. 1 Study area in Lugar Nuevo (LN) and Selladores-Contadero (SC), two enclosed official estates of 100 km^2 each. They are located separately in the Sierra de Andújar Natural Park in the Sierra Morena Mountains of Jaén, south-east Spain (38º9′N; 4º3′W and 38º23′N; 3º47′W, respectively)

Deer abundance estimates and hunting variables

A programme of regular management culls has been carried out in these estates since 1997 in order to reduce the deer densities and overabundance problems. Stalking has been the most used method of selective harvesting, focusing the cull management on hinds, calves and the poorly-antlered males in both species. A greater hunting effort was implemented for fallow deer, aiming at a significant population reduction of this species. Simultaneously, a standardized system was established to monitor changes in population size using direct counts through linear transects to be later analyzed through distance-sampling methods (Buckland et al. 2004). The survey design was established in order to achieve sufficient replicate lines and ensure that variations in encounter rates could be adequately estimated. Covering as many types of habitats as possible, sampling in a similar proportion, observations were made through lineal transects of 20 kilometres, using 5 forest tracks in LN and 4 in SC. Every year, during 3 consecutive days, 15 lineal transects in LN (300 km of road) and 12 transects in SC (240 km of road) were surveyed before the hunting season (in late September-early October). Transects were surveyed, by two experienced observers using four-wheel drive vehicles in the same way, under the same conditions every year. The total number of deer seen per year from 1999 to 2014 was recorded as an index of abundance to be used in a Bayesian state-space model together with the results of the harvest recorded as deer hunted per year.

Climatic variables

The study area is characterised by a Mediterranean-type macroclimate with irregular distribution of rainfall throughout the year, reaching the highest rates in spring and autumn–winter, and an almost total lack of rain with high temperatures during summer. Local weather measurements such as data on monthly precipitation and temperature were taken from local weather stations (located in the reserves themselves) and provided by the State Meteorological Agency (AEMET). From these data we estimate the Gaussen Index (GI) for spring (March–May), summer (June–August) and autumn (September–November) as the total amount of precipitation (in mm) minus twice the mean temperature (in °C) (Dajoz 2006). The Gaussen Index is a measure of the water available for vegetation, and can therefore be used as a proxy for resource availability (Imperio et al. 2011). Since it integrates temperature and rainfall it can also give us information about environmental constraints regarding corporal thermoregulation (Van Moorter et al. 2009). After checking climatic factors (see Fig. 2), weather indices of the previous years were used to test their effects on population growth rates.

Bayesian state-space model for population dynamics

The discrete population growth rate is usually defined as: $r_t = \log(N_t/N_{t-1})$ where r_t is the per capita rate of change realized between times $t-1$ and t. One model

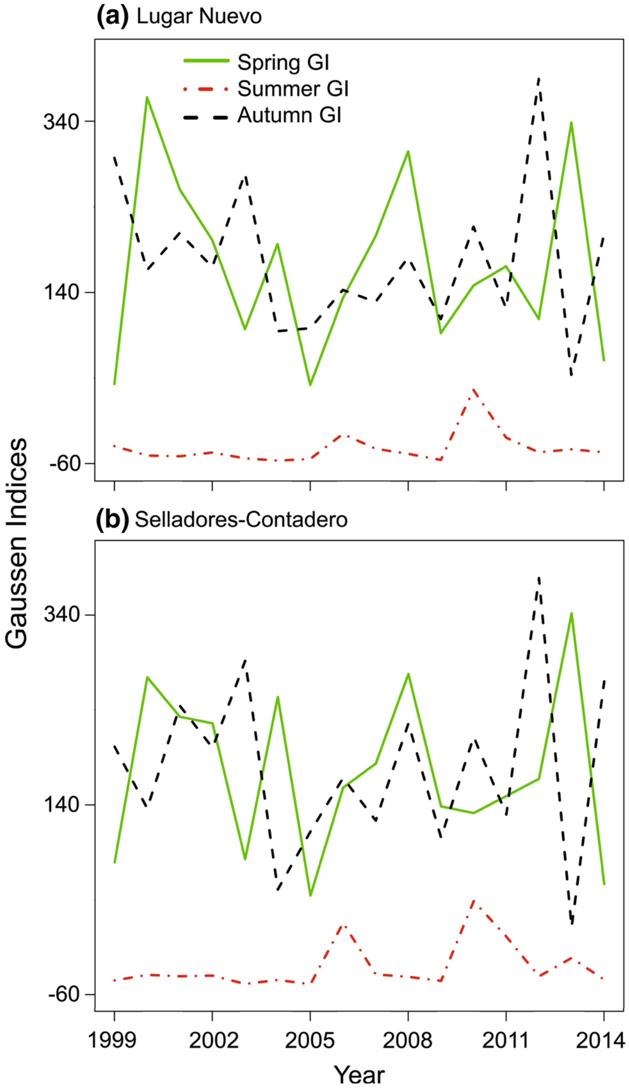

Fig. 2 Time series of the Gaussen indices through 16 consecutive years in two reserves, **a** Lugar Nuevo (LN) and **b** Selladores-Contadero (SC)

used to detect DD is the stochastic Gompertz model, defined as:

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

where the residuals ε_t are taken as Gaussian and uncorrelated. We used this model to test for the presence of DD (a negative slope b and one significantly different from zero indicate direct DD; Turchin 2003). Following the framework of the state-space model (Dennis et al. 2006), the Gompertz model becomes linear by

$$\left\{\begin{array}{l} X_t = X_{t-1} + a + bX_{t-1} + \varepsilon_t \\ Y_t = X_t + \eta_t \end{array}\right\}$$

X_t is the log scale of unobserved true population size ($X_t = \log N_t$), Y_t is the observed population size, and $\varepsilon_t \sim N\left(0, \sigma_p^2\right)$ and $\eta_t \sim N(0, \sigma_o^2)$ are the error terms with variance σ_p^2 and sampling variance σ_o^2 respectively.

We predicted that density dependence and hunting have been the primary drivers of population dynamics, and therefore we had to incorporate the effect of hunting (H) into the model (Iijima et al. 2013; Iijima and Ueno 2016), where $e_{t-1} = \log(1 - H_{t-1}/N_{t-1})$ is the logarithmic integration of hunting occurring in the season following the survey at $t-1$.

Therefore $X_t = X_{t-1} + e_{t-1} + a + b(X_{t-1} + e_{t-1})$.

To introduce the effect of climate variables, we decided to use a similar version of the Bayesian state-space model used in Koons et al. (2015), therefore

$$X_t = X_{t-1} + e_{t-1} + \beta_0 + \beta_1(X_{t-1} + e_{t-1}) + \sum_{i=1}^{3} \beta_{i+1} Z_{t-1}^{(i)} + \varepsilon_t$$

where β_0 and β_1 are the parameters for a and b respectively, and β_{i} are the parameters for climatic covariate $Z^{(i)}$. The errors ε_t are defined as above. We fit all the possible combinations of Bayesian state-space models, for red and fallow deer each one being differentiated by the climatic covariate; spring $(Z^{(1)})$, summer $(Z^{(2)})$ and autumn $(Z^{(3)})$ GI. We used $Y_t \sim \mathrm{Poisson}(\exp(X_t))$ to model observation error in the counts, which is naturally suited for discrete random variables like population counts.

State-space models can be divided into state processes and observation processes. The state-process, denoted as X_t, with $t = 0, 1, \cdots, T$, is an unobservable vector that expresses the stochastic evolution of ecological states. When analyzing population dynamics a first-order Markov process, $X_t | X_{t-1}$, is generally applied. The observation process, denoted as Y_t, is an observable vector that is related to X_t but fluctuates with observation error. These processes have uncertainties, which are described as a set of three probability distribution functions (pdfs): $\phi_t(X_t | X_{t-1}; \alpha)$ is the state process pdf, $\phi_0(X_0; \mu)$ is the initial state pdf and $\psi_t(Y_t | X_t; \gamma)$ is the observation process pdf, where $\theta = (\alpha, \mu, \gamma)$ are the parameters of the model.

Model implementation and Goodness-of-fit

Under a Bayesian context, the inference objective for a state-space model draws samples from the joint posterior distribution for the state variables X and unknown parameters θ, conditional on the observed time-series data Y. If we denote the prior pdf of the model parameters as $\pi(\theta)$, the joint posterior pdf can be expressed as

$$\pi(X|Y) \propto \pi(\theta)\phi_0(X_0; \mu)\left(\prod_{t=1}^{T} \phi_t(X_t | X_{t-1}; \alpha)\psi_t(Y_t | X_t; \gamma)\right).$$

We adopted this Bayesian approach by using the Markov Chain Monte Carlo (MCMC) method (Gelfand and Smith 1990) in JAGS 3.3.0 (Plummer 2012), run from the R2Jags package implemented in R.3.1.1 (R

Development Core Team 2014). For each model we ran three parallel MCMC chains and retained 1,000,000 iterations after an initial burn-in of 500,000 iterations. We then thinned the samples by keeping every 50th sample. Convergence of MCMC sampling was judged by the criterion that $\hat{R}$ was smaller than 1.1 (Gelman et al. 2004), along with traceplots, to monitor chain convergence. The R code with our Bayesian state-space model is available as Electronic Supplementary Material (ESM1).

Prior distributions

In accordance with Gelman (2006), we adopted a vague prior for: $\beta_0, \beta_1, \beta_2, \beta_3, \beta_4 \sim \mathrm{N}(0, 1000)$, and the prior for process variance is modeled as $\sigma_p \sim \mathrm{U}(0, 100)$. However, we assumed that β_0 can never exceed log(2), because the abundance never doubles in a year, even if all were females with a 100% pregnancy rate (Iijima and Ueno 2016). The prior for β_1 is truncated at -2 and 2 in order to exclude impossibilities, because the population will experience standard density dependence when $-2<\beta_1<0$, but at 0 density independence occurs. Values of $\beta_1<-2$ would indicate that density dependence is so strong that this would lead to unstable chaotic population dynamics, and above 0 density has a positive effect on population growth (Dennis et al. 2006; Koons et al. 2015). In order to check the overdispersion problem we can obtain Pearson residuals. The simplest way is to take the mean values from the MCMC samples and use these to calculate the Pearson residuals, but it is more informative to calculate the Pearson residuals for each MCMC realization individually. In addition, we can also generate 'predicted' residuals for each MCMC realization obtained from simulating abundance data from a Poisson distribution. The latter will be properly Poisson-distributed, so it will not display any overdispersion (Zuur et al. 2009). We have checked that our state-space models do not present the overdispersion problem. Outputs for the overdispersion tests are available as Electronic Supplementary Material (ESM2), and the outputs of the Bayesian state-space model for our population dynamic are available as Electronic Supplementary Material (ESM3).

Results

A set of models explaining the population dynamics are summarized in Tables 1 and 2, including parameters such as intrinsic rate, density-dependence and climate for red a fallow deer in both reserves respectively.

Red deer population dynamic

For the red deer in the LN reserve we only found one model with significant effects of density dependence. Model 2 (Table 1) presents a posterior mean of $\beta_0 = 0.375$, sd = 0.198, 95% CI = (0.024, 0.680) with statistically significant effects, indicating strong potential for population growth based on the Bayesian credible interval at 95%. The posterior mean of the density dependence variable is $\beta_1 = -0.066$, sd = 0.039, 95% CI = (−0.138, 0.009), with effects being statistically significant based on the Bayesian credible interval at 90%, and the posterior mean of climatic spring GI variable is $\beta_2 = 0.001$, sd = 0.001, 95% CI = (−0.001, 0.003) with non statistically significant effects. The rest of the LN models for red deer only present one statistically significant parameter, the intrinsic rate.

For red deer in the SC reserve we found two models (model 2 and 3) with significant effects of density dependence and a positive effect of spring GI. For example model 2, Table 1, with posterior mean of $\beta_0 = 0.377$, sd = 0.198, 95% CI = (0.021, 0.679) with

Table 1 Bayesian state-space models explaining population growth for red deer (*Cervus elaphus hispanicus*) in two hunting reserves of Southern Spain

Model	Explicative variables	Lugar Nuevo	Selladores-Contadero
1	Intrinsic rate $t-1$	0.3756 **(0.0233, 0.6786)**[a]	0.3926 **(0.0250, 0.6813)**[a]
	Density dependence $t-1$	−0.0416 (−0.0950, 0.0174)	−0.0238 (−0.0845, 0.0445)
2	Intrinsic rate $t-1$	0.3745 **(0.0235, 0.6796)**[a]	0.3766 **(0.0214, 0.6790)**[a]
	Density dependence $t-1$	−0.0662 **(−0.1376, 0.0091)**[b]	−0.0925 **(−0.1780, −0.0044)**[a]
	SpringGI $t-1$	0.0009 (−0.0008, 0.0026)	0.0026 **(0.0003, 0.0048)**[a]
3	Intrinsic rate $t-1$	0.3736 **(0.0218, 0.6797)**[a]	0.3732 **(0.0216, 0.6794)**[a]
	Density dependence $t-1$	−0.0765 (−0.1681, 0.0192)	−0.0907 **(−0.1849, 0.0075)**[b]
	SpringGI $t-1$	0.0009 (−0.0009, 0.0027)	0.0026 **(0.0026, 0.0049)**[a]
	SummerGI $t-1$	−0.0018 (−0.0109, 0.0072)	0.0004 (−0.0073, 0.0081)
4	Intrinsic rate $t-1$	0.3694 **(0.0207, 0.6798)**[a]	0.3612 **(0.0188, 0.6779)**[a]
	Density dependence $t-1$	−0.0348 (−0.1600, 0.0948)	0.0057 (−0.1018, 0.1143)
	SpringGI $t-1$	0.0006 (−0.0013, 0.0025)	0.0017 **(−0.0002, 0.0036)**[b]
	SummerGI $t-1$	−0.0012 (−0.0105, 0.0080)	−0.0002 (−0.0060, 0.0058)
	AutumnGI $t-1$	−0.0011 (−0.0034, 0.0012)	−0.0027 **(−0.0046, −0.0008)**[a]

From left to right: model, explicative variables, posterior mean value of parameters with their 95% credible intervals for both reserves

[a] In bold significant effect whose 95% CI does not overlap with zero, [b] in bold marginal effect whose 90% CI does not overlap with zero, *GI* Gaussen indice

Table 2 Bayesian state-space models explaining population growth for fallow deer (*Dama dama*) in two hunting reserves of Southern Spain

Model	Explicative variables	Lugar Nuevo	Selladores-Contadero
1	Intrinsic rate $t-1$	0.5819 **(0.3384, 0.6896)**[a]	0.4784 **(0.0682, 0.6866)**[a]
	Density dependence $t-1$	−0.0242 **(−0.0711, −0.0009)**[a]	0.0504 (−0.1247, 0.2484)
2	Intrinsic rate $t-1$	0.5150 **(0.1274, 0.6878)**[a]	0.4474 **(0.0488, 0.6849)**[a]
	Density dependence $t-1$	−0.0479 **(−0.1490, −0.0016)**[a]	−0.2160 (−0.4892, 0.0507)
	SpringGI $t-1$	0.0014 (−0.0009, 0.0044)	0.0058 **(0.0013, 0.0107)**[a]
3	Intrinsic rate $t-1$	0.4475 **(0.0561, 0.6842)**[a]	0.4164 **(0.0324, 0.6831)**[a]
	Density dependence $t-1$	−0.0940 **(−0.2241, −0.0064)**[a]	−0.2031 (−0.4658, 0.0474)
	SpringGI $t-1$	−0.0003 (−0.0028, 0.0025)	0.0041 **(−0.0007, 0.0093)**[b]
	SummerGI $t-1$	−0.0168 **(−0.0295, −0.0054)**[a]	−0.0120 (−0.0290, 0.0043)
4	Intrinsic rate $t-1$	0.4655 **(0.0600, 0.6861)**[a]	0.4147 **(0.0326, 0.6831)**[a]
	Density dependence $t-1$	−0.0874 **(−0.2584, −0.0032)**[a]	−0.1749 (−0.5238, 0.1665)
	SpringGI $t-1$	−0.0003 (−0.0029, 0.0026)	0.0041 **(−0.0012, 0.0096)**[b]
	SummerGI $t-1$	−0.0176 **(−0.0310, −0.0056)**[a]	−0.0130 (−0.0324, 0.0059)
	AutumnGI $t-1$	−0.0005 (−0.0032, 0.0028)	−0.0007 (−0.0060, 0.0046)

From left to right: model, explicative variables, posterior mean value of parameters with their 95% credible intervals for both reserves
[a] in bold significant effect whose 95% CI does not overlap with zero, [b] in bold marginal effect whose 90% CI does not overlap with zero, *GI* Gaussen indice

significant effect, indicating strong potential for population growth, the posterior mean of the density dependence variable is $\beta_1 = -0.093$, sd = 0.045, 95% CI = (−0.178, −0.004) with weak but statistically significant effects and the posterior mean of the climatic spring GI variable is $\beta_2 = 0.003$, sd = 0.001, 95% CI = (0.0003, 0.005) with weak but statistically significant effects. Other potential models include the autumn GI variable with significant negative effect $\beta_4 = -0.003$ (see model 4, Table 1).

Fallow deer population dynamic

For the fallow deer in the LN reserve we found that all models implemented present significant effects of density dependence and negative effects of summer GI. For example model 3, Table 2, presents a posterior mean of $\beta_0 = 0.448$, sd = 0.180, 95% CI = (0.056, 0.684) with statistically significant effects, indicating strong potential for population growth based on the Bayesian credible interval at 95% The posterior mean of the density dependence variable is $\beta_1 = -0.094$, sd = 0.058, 95% CI = (−0.224, −0.006) with statistically significant effects, the posterior mean of climatic summer GI is $\beta_3 = -0.017$, sd = 0.006, 95%CI = (−0.030, −0.005).

For fallow deer in the SC reserve we found that no model presents significant effects of density dependence, having detected a positive effect of spring GI. For example model 2, Table 2, presents a posterior mean of $\beta_0 = 0.447$, sd = 0.184, 95%CI = (0.049, 0.685), with significant effect, indicating strong potential for population growth, the posterior mean of the density dependence variable is $\beta_1 = -0.216$, sd = 0.135, 95% CI = (−0.489, 0.051) having no statistically significant effects, and the posterior mean of the climatic spring GI variable is $\beta_2 = 0.006$, sd = 0.002, 95% CI = (0.001, 0.011) with significant effects.

Discussion

We investigated the population dynamics drivers of sympatric red and fallow deer in two separate reserves in a Mediterranean ecosystem, these being intra-specific competition together with factors such as hunting and weather. Studying sympatric deer in two separate populations allows us a better assessment of the effects of density and hunting pressure in the same climatic regime. To our understanding, this paper presents for the first time a system for monitoring the deer population dynamics in the south of the Iberian Peninsula for nearly two decades and the effectiveness of selective culling in controlling population size, considering climatic and density-dependence effects. Our completive time series of 16 successive years appears inside the range of years in similar studies (Knape and de Valpine 2012), and no previous studies are based on time series analysis of nearly two decades in our area. From a methodological point of view in DD detection, not many papers represent such a broad approach as this study, using the most recent advances in Bayesian inference. Through an integrative Bayesian state-space modeling making possible a unified population analysis we are able to not only estimate the effects of density dependence, climate and harvest extractions but also to evaluate their relative impacts on red and fallow deer population in each location.

A general fit between predicted estimates of annual deer abundance based on Bayesian state-space models and observed values (open circles) in the time series of the population trend of red deer (*Cervus elaphus hispanicus*) and fallow deer (*Dama dama*) is shown in Fig. 3, together with the harvest rates through 16 consecutive years.

We found all our deer populations exhibiting a very strong potential to grow from low density. We detected

DD having a stronger effect than hunting and climatic factors for fallow deer in LN and also red deer in SC, maybe because these populations are in an overabundant situation close to their carrying capacity. Both the red deer population in SC and the fallow deer in LN have fluctuated over the years, but they may be considered without a net reduction or population size variation from 1999 to 2014, despite the high harvest rates. This may be explained because of the existence of density-dependent mechanisms which compensate harvest extractions, reducing hunting effectiveness. In contrast, the red deer population in LN tended to decrease whereas a great increase of fallow deer in SC was observed in the last years despite the hunting.

Preliminary studies also reported the culling level applied between 2002 and 2009 reducing red deer densities minimally but with no effect on fallow deer population size, although the implication of the possible self-regulatory mechanisms cannot be measured because density-dependence was not considered at that time (Nugent et al. 2011).

As expected, the Bayesian state-space models do not demonstrate the presence of DD for fallow deer in SC, maybe because this population is still below the carrying capacity. Detection of DD will require the study of a population close to its ecological carrying capacity where DD is likely to be strongest (McCullough 2001), and this does not seem to be the case of fallow deer in SC. We also found less effectiveness of culling in controlling the population size of red deer in SC and fallow deer in LN where more DD was detected ($\beta_1 = -0.093$ in model 2 for red deer in SC and $\beta_1 = -0.094$ in model 3 for fallow deer in LN, Table 1 and 2, respectively).

A key insight obtained from the logistic growth model is that under the assumption of DD decreased crowding should improve survival. This is the reason why harvesting may be considered a sustainable resource. At any population size below the carrying capacity the population produces a surplus yield available for harvesting without a reduction of population size. Removing only the surplus leads to a compensatory mortality which is not sustainable in order to reduce population density.

Because of possible DD changes which could compensate for losses to harvesting hunting effectiveness remains reduced, making it necessary to maintain deer extraction levels above a given threshold in order to achieve additive mortality and so reduce the population size. Our results agree with those of Ueno et al. (2010) which showed that high hunting mortality with intensive harvesting was necessary to prevent population growth. In fact, management efforts to reduce abundance have been directed at increasing mortality via hunting and culling operations in this area. However, the results of monitoring deer populations show that the red deer population in LN tends to decrease, whereas both the red deer in SC and fallow deer populations in LN have fluctuated over the years, but they may be considered

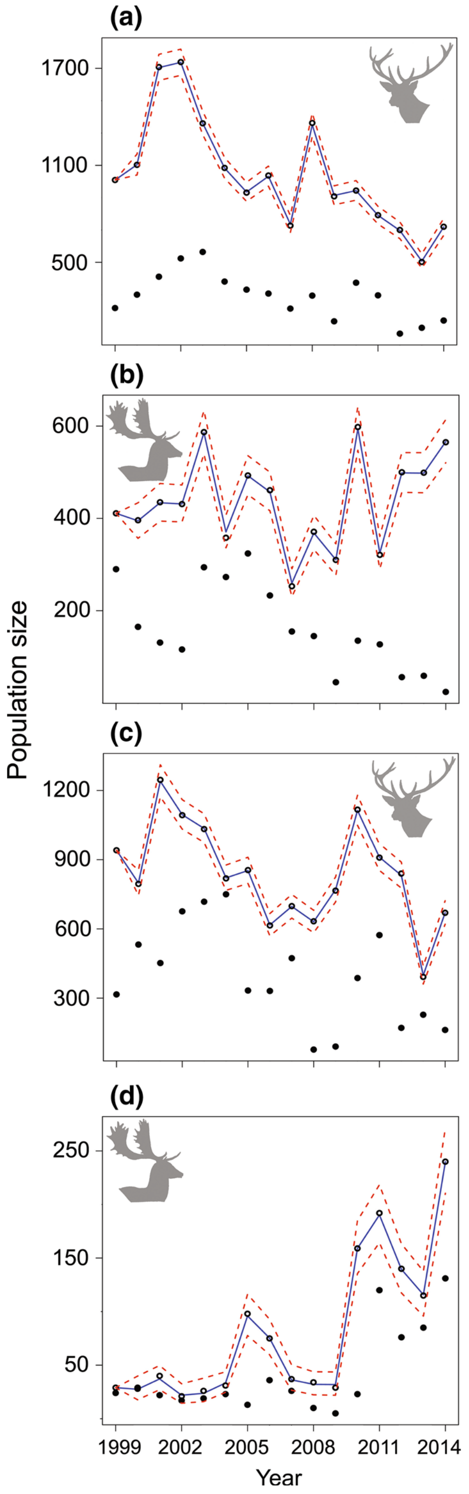

Fig. 3 Time series of the population trend of red deer (*Cervus elaphus hispanicus*) and fallow deer (*Dama dama*) through 16 consecutive years, from 1999 to 2014, (**a**) and (**c**) for red deer, (**b**) and (**d**) for fallow deer in Lugar Nuevo (LN) and Selladores-Contadero (SC), respectively. Predicted estimates of annual red or fallow deer abundance (*solid line*, with 95% credible intervals denoted by *dashed lines*) relative to observed (*open circles*) based on the full Bayesian state-space model. The annual number of hunting extraction from the populations (*solids circles*) is shown on the *right* axis

without a net variation or population size reduction (Fig. 3). Also Putman et al. (2005) found compensation mechanisms in harvested populations leading to populations of a similar size to that before harvesting. Our results are also in keeping with studies of deer species of North America in a Mediterranean environmental climate such as in California. These populations showed that the DD response was robust enough to be measured, and used to advantage in harvest programs (McCullough 2001). When DD occurs hunting is believed to be less effective in population control probably because of a reduction in population relieving intraspecific forage competition, leading to performance and reproduction increases and a subsequent rapid new population growth. Thus harvests should be managed considering the compensatory effects of alleviating density, with intensive harvesting and global deer extraction levels above the thresholds for additive mortality being necessary to reduce the population size.

In this arid Mediterranean environment where there are more severe drought and aridity conditions during the summer than in other Mediterranean environments such as those reported in Italy (Imperio et al. 2011), we expected summer drought to affect population growth greatly. Water availability, which is related to food availability and quality, seems to be an important restrictive factor of the population growth rates, contrasting with the cold temperatures during winter in colder areas (Fowler 1987; Coulson et al. 2000; Post 2005). Greater water availability during spring was expected to be a positive driver in increasing growth rates as this affects positively the quantity of food available to female ungulates during gestation and lactation (Rodríguez-Hidalgo et al. 2010). Due to a higher aridity in summer we expected the strong effects of climatic conditions to modulate the DD strength similarly to those reported in northern populations (Aanes et al. 2000). Surprisingly, in our study climate plays a significant but weak role in deer population dynamics, with intraspecific competition being the more important driver and the worst effects of climatic constraints being detected when more DD populations occur. No effect of weather or a positive effect of rainfall in spring were detected in populations with a weak DD like red deer (Table 1) or with no DD detected like for fallow deer in SC (see Table 2).We found a slight positive effect of the spring Gaussen Index on the population growth rate in red and fallow deer from SC (Tables 1 and 2 respectively). However, a negative relationship was found between the autumn Gaussen Index and the population growth rate of red deer in SC (models 3 and 4, Table 1), as well as a higher negative effect of the summer Gaussen Index on the fallow deer population growth in LN (models 3 and 4, Table 2).

In our study summer drought has been shown to have a delayed effect on the dynamics of deer through the loss of physical condition that leaves the weak deer to support the constraints of the first autumn rains. Probably the simultaneous occurrence of the first rainfalls on deer with a very weak body condition after the summer makes them incapable of regulating even their body temperature, and death occurs. The results should be understood along with other studies related to diet quality and body or health condition (e.g. Azorit et al. 2012a, b).

Through our integrative analysis a strong potential to grow from low density is detected for both deer species, (for red deer ranging from $\beta_0 = 0.360 - 0.393$ and even higher for fallow deer, ranging from $\beta_0 = 0.415 - 0.582$), implying that the local ecosystems can support a robust deer population, even if the upper limit of posterior β_0 is determined by the prior setting. As we explained before, we assumed that β_0 can never exceed $\log(2)$, because the abundance never doubles in a year, even if all were females with a 100% pregnancy rate (Iijima and Ueno 2016). In any case, we found density-independent regulation more important the more abundant the deer are or at least when the populations are closer to their carrying capacity. This is observed especially in the red deer population in SC and fallow deer population in LN (Tables 1 and 2 respectively). Deer populations with less density-dependence and less competition for resources take advantage of spring rains to promote good body condition. Then they are able to cushion the summer constraints and reach autumn in better body condition and compensate for the severe drought conditions during the summer which may cause delayed deer deaths in autumn. This is important to consider regarding climate change, as population densities must be well controlled in order to prevent the negative effects of aridity and climatic events.

In conclusion, the Bayesian state-space model appears as a unified population analysis model where the hunting processes can be considered explicitly, as well as information regarding climatic and population factors which have helped us in understanding population dynamics. We detected DD to have a stronger effect than hunting and climatic factors, especially for deer overabundant populations close to their carrying capacity. Density-dependent mechanisms compensate harvest extractions, reducing hunting effectiveness in these populations. Severe summer drought conditions had negative effects on growth rates and eventually led to delayed autumn deer deaths. In the context of climate change, in Mediterranean environments the importance of weather factors could become much greater if both densities of ungulates and aridity increase. Population size control here could modulate the negative effects of climatic constraints on deer condition and ecosystems conservation.

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