Biotic and abiotic factors modulating wild boar relative abundance in Atlantic Spain

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Abstract

The population dynamics of wild ungulates, particularly wild boar (*Sus scrofa*) are modulated by biotic (e.g. predation) and abiotic (environmental) determinants. Iberian wolf (*Canis lupus signatus;* hereafter wolf) is considered the main predator of wild ungulates and wild boar is one of the most important components of its diet in Atlantic Spain. Despite the evident potential interference of predation in the environmental patterns of wild boar population abundance, studies including both predation and abiotic factors are scarce. Here we tested the effects of predation and environmental characteristics on wild boar relative abundance using spatially explicit predictive models. Variation partitioning procedures were used to investigate the relative importance of each factor and their overlaid effects. Wild boar relative abundance was determined by hunting bag statistics, including hunting effort related-variables (in order to avoid problems derived from modeling rates) as covariates, while wolf attacks to livestock were considered as a proxy of wolf frequency in the drive. Our results suggested that a great deal of the variability in wild boar abundance can be explained by wolf relative abundance. The relevance of this factor can be explained by the high predation rates of wolf on juvenile wild boar. According to previous knowledge on the wild boar ecology, our results showed that the species abundance is positively influenced by the percentage of surface occupied by mature forest and heather providing high food diversity and refuge, but these environmental variables achieved a low explanatory capacity in the models in relation to wolf frequency. The holistic approach followed in this study was attended to open new perspectives for thinking on the wolf-livestock conflict and to adequate wild boar management strategies taking into account hunting interests and natural processes.

Keywords*: Canis lupus signatus*, habitat structure, land use, spatially explicit model, *Sus scrofa*.

Introduction

Populations of wild ungulates in general and wild boar (*Sus scrofa*) in particular, have been expanding during recent decades across Europe, both in density and in geographical range (Saez- Royuela and Tellería 1986; Gortázar et al. 2000; Apollonio et al. 2010). Interspecific relationships –including predation–, reproduction, environmental characteristics and hunting, modulate wild ungulate population dynamics (Okarma 1995; Latham 1999; Acevedo et al. 2006; Apollonio et al. 2010; Fonseca et al. 2011; Servanty et al. 2011; Keuling et al. 2013). Ungulates, whilst being major consumers of vegetation, are themselves consumed by predators, revealing much about dominant trophic linkages in terrestrial systems (Schmitz et al. 2000; Peterson 2003). Whereas the actual dynamics of predator-ungulate interaction can be determined by preferred prey species and predator abundance (Latham 1999; Nowak et al. 2005; Barja 2009; Davis et al. 2012), the habitat-ungulate interaction is mainly determined by habitat composition and structure (Abaigar et al. 1994). Thus, predator-related features and habitat characteristics should be considered in unison when studying the population dynamics of wild ungulates.

The wolf (*Canis lupus*) is usually considered the main predator of ungulates (Jedrzejewski et al. 1992; Nowak et al. 2005; Valdmann et al. 2005). In fact, the wild boar has been identified as the main food resource in the wolf diet in many studies in Europe (e.g. Cuesta et al. 1991; Meriggi and Lovari 1996; Capitani et al. 2004; Nores et al. 2008; Barja 2009; Wagner et al. 2012), reflecting the wolf's opportunist character, preying on the more abundant preys (Glasser 1982; Salvador and Abad 1987), but in other instances indicating sometimes the preference of wild boar (e.g. Fernández-Gil 2004; Davis et al. 2012). In this respect, Nores et al. (2008) estimated that wolf predation causes 12% of wild boar mortality in Atlantic Spain. Thus, close relationships between the population dynamics of both wolf and wild boar can be expected. For instance, it has been found that when wolf populations decrease, wild boar populations tend to increase (Sáez-Royuela and Tellería 1986; Gerard et al. 1991). But this is not an inflexible rule since a limited effect of wolf numbers on wild boar populations has been detected in other studies (e.g. Melis et al. 2006).

The association between wolf and wild ungulates may be an important piece for mediating in the wolf-livestock conflict (Fritts and Mech 1981; Jhala 1993; Gazzola et al. 2005; Nowak et al. 2005; Barja 2009; Hosseini-Zavarei et al. 2013). The abundance, richness and diversity of wild ungulates is related to livestock consumption (Meriggi and Lovari 1996), such that there is a reduction in wolf attacks on livestock in areas where ungulates are abundant and diverse (see also Meriggi and Lovari 1996; Urios et al. 2000; Sidorovich et al. 2003). At this level, ungulate abundance at large spatial scales is modulated by habitat. The relationships between wild boar population abundance and habitat characteristics, despite the generalist character of the species, are well determined (Taylor et al. 1998; Cahill et al. 2003; Acevedo et al. 2006; Herrero et al. 2006) and wild boar selects heterogeneous landscapes, dominated by mature forest, that provide high food diversity and refuge (Abaigar et al. 1994; Fernández-Llario 2004; Acevedo et al. 2006).

Data of wildlife population abundance is not easy to record for large spatial scales. Thus, indirect methods are commonly used, in particular for elusive species such as wild boar and/or wolf (reviewed by Llaneza et al. 1998; Engeman et al. 2013). For instance, hunting bag derived-statistics are the most widely employed indirect indices to determine wild boar relative abundances due to the method's low cost and simplicity, and the feasibility of carrying out studies at large spatial-temporal scales (e.g. Sáez-Royuela and Tellería 1986; Acevedo et al. 2006, 2011; Rodríguez-Prieto et al. 2012).

Despite their limitations, when hunting effort is taken into account, these indices produce a reliable estimation of wild boar population abundance at both local and large spatio-temporal scales (Acevedo et al. 2007; Imperio et al. 2010). Wolf abundance can be estimated with direct methods rather than indirect ones or, indeed, with a combination of both, the latter being highlighted by Llaneza et al. (1998) as the most effective procedure. In addition, while it is true that more reliable estimates of wolf abundance are obtained from direct methods, an index based on the number of livestock attacks by wolves can be used to roughly estimate wolf relative abundance (Kusak et al. 2005; Hosseini-Zavarei et al. 2013), by considering the availability of livestock as the most important factor determining wolf frequency (Uzal and Llaneza 2010; Eggerman et al. 2011). Livestock attacks largely correspond to confirmed wolf presence (Pimenta et al. 2005) and are considered a useful tool to assess the presence of dispersed individuals, the emergence and establishment of the wolf in new areas, and also in feeding studies (Dos Santos Reis and López 1997; Alexandre et al. 2000; Urios et al. 2000).

As previously stated, numerous studies have assessed the effects of predators or habitat on wild boar abundance but, in contrast, studies that simultaneously include these two factors are scarce (but see Melis et al. 2006). In this context, the aim of our study was to, firstly, investigate the effects of habitat features which modulate the relative abundance of wild boar populations and, secondly, how the abundance of boars is related to frequency of wolf attacks in the area. The analysis of these complex systems attempts to open up new perspectives for thinking about the wolf-livestock conflict (see Treves et al. 2004).

Materials and methods

Study area

This study was conducted across Asturias, a province located in northwestern Spain, during September-February 2007-2010. Specifically, data were collected in the Regional Game Reserves (RGRs; Figure 1) located throughout the Cantabrian Mountains, which include several protected areas and threatened and diverse fauna such as Brown bear *Ursus arctos*, Cantabrian capercaillie *Tetrao urogallus* and Iberian wolf *Canis lupus signatus* (hereafter wolf).

RGRs are characterized by an Atlantic climate. In medium elevation (500-1500 m) areas, deciduous mixed forests are predominant with beech *Fagus sylvatica*, chestnut *Castanea sativa*, oak *Quercus robur*, *Q. petraea*, *Q. pyrenaica*, *Q. orocantabrica*, holly *Ilex aquifolium* and hazel *Corilus avellana*. However, higher areas (>1500 m) are dominated by broom, scrub and heather: *Genista* spp.*, Cytisus* spp.*, Erica* spp., *Calluna* spp.*, Vaccinium* spp.*, Juniperus* spp.

Wild boar relative abundance index and hunting methodological variables

To estimate wild boar abundance it is not an easy task. At large spatial-temporal scales hunting bag statistics are the most recommendable, cost-effective and suitable option (e.g. Boitani et al. 1995; Imperio et al. 2010), since the information is freely available at no cost, and only requires the information to be registered and centralized on a database (Sáez-Royuela and Tellería 1986; Acevedo et al. in press). Acevedo et al. (2009) pointed out the importance of hunting effectiveness to estimate wild boar abundance by using these kinds of indices, and they suggested that as effectiveness varied between areas, more precise estimations can be obtained if the number of boars seen –instead of the number of animals hunted– was considered. In this study the number of wild boar seen in each battue was considered as our response variable. We obtained data from 704 battues during the 2007-2010 hunting seasons. Since the 2007/2008 hunting season, for each wild boar battue the game wardens in the RGRs have systematically recorded number of seen boars, hunting effort (number of hunters, beaters and dogs) and the drive (our territorial sampling unit; Figure 1) in their activity reports. In the Cantabrian Mountains, each battue is conducted on a given drive (n=268) –the small area of each individual hunt–, which is within a hunting area (n=46), which is in turn part of an RGR (n=11); in other words, an RGR contains several hunting areas and each one contains several drives. RGRs, hunting areas and drives are georeferenced.

Our wild boar data represents raw information on the number of wild boars seen, i.e., it is not standardized by sampling effort. Several studies have pointed out potential problems associated with the use of ratios –as the standardized indices– when performing statistical models and they suggest directly modeling the numerator as response variable but including the denominator as covariate/s in the model (e.g. Kronmal 1993). Thus, for modeling purposes we included variables accounting for sampling effort and sampling period as covariates. These hunting methodological variables were; total number of hunters, beaters and dogs (10-31), surface area of the drive (range: 5-600 ha), and month (from September to February).

Environmental characteristics: vegetation and topography

For each drive we extracted environmental variables to be used as predictors of the variations in wild boar relative abundance from the thematic regional cartography (GIS of the Environmental Thematic Cartography, 1:25000 scaled, Environmental Agency of Asturias, 1997). Seven different vegetation classes (quantified as percentage of surface occupied by each class) were used as predictors in line with previous studies on the environmental factors determining wild boar abundance (e.g. Acevedo et al. 2009, in press): mature forest (mainly oak and beech), pre forest, broom and scrub, heather, tree plantations, fern and meadows. In addition habitat diversity in each drive was calculated using Shannon´s diversity index (see McGarigal and Marks 1995). Finally, the topographic data, average altitude (m a.s.l), average slope (percentage) and south-west orientation (percentage of surface occupied by this orientation class; Fernández-Llario 2004; Acevedo et al. 2009) were extracted for each drive from a digital elevation model grid (spatial resolution of 30 m; ASTER Global Digital Elevation Model V001) (Japanese Ministry of Economy, Trade and Industry and N.A.S.A.).

Wolf frequency

In order to take into account the abundance of predator on wild boar-habitat relationships, we included, as predictor, a proxy of wolf frequency in the drive; it being the main wild predator of wild boar in Spain (Nores et al. 2008). Wolf frequency was quantified from the livestock-attack reports of the Environmental Agency of Asturias game wardens in the RGRs, a valuable tool to locate and identify individuals and reproductive units, and as a proxy for describing their movements and territories (Dos Santos Reis and López 1997; Alexandre et al. 2000). Particularly in Asturias, livestock-attack data of wolf attacks to livestock are recognized as highly reliable (Talegon and Gayol 2010). Each attack location was georeferenced and assigned to the drives within a 2.5 km radius, according to the wolf´s area of activity (Ciucci et al., 1997; Jedrzejewski et al. 2002; Kusak et al. 2005; Llaneza et al. 2011). Wolf frequency was calculated as the sum of the wolf attacks on livestock per month during the hunting season

(September to February) (Kusak et al. 2005; Eggerman et al. 2011; Hosseini-Zavarei et al. 2013).

Statistical analysis

To study the differential effects of habitat composition and structure, and wolf frequency modulation on wild boar population abundance, we performed Generalized Linear Mixed Models (GLMMs) with a Poisson distribution and logarithmic link function. The most parsimonious models were selected using a backward stepwise procedure based on Akaike Information Criteria (AIC; Akaike 1974). We considered those models separated by less than 2 AIC points as having similar strength evidence (Burnham and Anderson 2002). Territory (RGR, hunting area and drive, were all nested and considered as a single variable) and hunting season was considered as random factor. In addition, the methodological variables (period, surface area and hunting effort), the environmental ones (habitat composition and structure) and wolf frequency were considered as fixed factors. All statistical analyses were performed with the software R 12.1 (R DevelopmentCore Team 2006), package 'lme4' (Bates et al. 2012).

Finally, to enhance the explanatory power of the models we performed variation partitioning procedures (Borcard et al. 1992), in order to estimate the variation in the final models which were independently explained by each factor (pure effects) and the variation explained by two or more factors simultaneously (overlaid effects). It should be noted that each factor is a group of related-predictors; in this study we took into account three factors: methodology (Hm), environment (E) and wolf frequency (W). After the development of the final models (Hm+E+W), we modeled our response variable independently with variables related to each factor (Hm, E and W), as well as with each pair of factors (Hm+E, Hm+W and E+W) to obtain the partial models. We determined the variation explained by final and partial models in terms of explained deviance. These amounts of variation were then used in R package modEva in order to draw the diagram (Barbosa et al. 2013).

Results

Wild boar occurred in 85.2% of the drives, with numbers varying between 1 and 33 individuals seen per battue. Results of the four models separated by less than 2 AIC points are reported in Table 1, and they share most of the significant predictors. The explained deviance of the most parsimonious model was 10.76%; although the other three models showed a similar degree of explained deviance (10.75-11.03%).

In the four models selected we found significant associations between wild boar numbers and hunting methodological variables: period, surface area and hunting effort. The number of wild boars seen was higher in bigger drives with a higher hunting effort. In addition, the number of individuals seen increased during the period (highest in February). After controlling for methodological factors, we found a positive relationship between the surface area occupied by mature forest and heather and wild boar relative abundance. Elevation was negatively related to the response variable, lower wild boar relative abundance was observed in high elevation battues (in three of the four models). Finally wolf attacks on livestock occurred in 57.5% of the drives, with between 1 and 28 attacks per battue during the hunting season. A positive association between the relative abundance of wild boar and wolf attacks fequency was also detected in all four models.

Results of variation partitioning in the four models showed that the pure effect of wolf frequency explained the highest percentage of the explained deviance (65.4-67.5%)

followed by the pure effect of the methodological factor (21.1-22.6%). However, the habitat factor only explained between 6.2 and 8.0% of deviance (see Figure 2 and Appendix 2).

Discussion

This study evidences that a great deal of the variability in wild boar abundance, estimated through hunting bags, can be explained by wolf frequency and that predation was the main factor modulating wild boar population dynamics (Jedrzejewski et al. 1992; Mattioli et al. 1995; Kanzaki et al. 1998; Nores et al. 2008) followed by environmental characteristics, this latter being considered in many studies as the unique factor influencing distribution/abundance. The generalist character in habitat terms of the target species may, at a certain level, account for the large amount of unexplained deviance in our model, but is reasonable to assume that the potential effect of uncontrolled environmental factors plays a part.

On the methodological approach: hunting methodological variables

The most widely employed method to estimate wild boar relative abundance is based on hunting bag statistics standardized by hunting effort (see Sáez-Royuela and Tellería 1986; Acevedo et al. 2006, 2009, 2011; Engeman et al. 2013). These standardized indices have been assessed both at local (Acevedo et al. 2007) and at large spatio-temporal scales (Imperio et al. 2010; Acevedo et al. in press). Since there have been criticisms of the use of ratios (e.g. Kronmal 1993), in this study hunting methodological variables were included as covariates in the models rather than using only standardized hunting bag data, and raw data of the number of wild boar seen during the drive was used as response variable. This kind of analytical approach has recently been highlighted in the context of body condition measures (Serrano et al. 2008; see also Santos et al. 2013) and it has potential to be used in ecological modeling.

Biotic interactions and abiotic requirements

Many studies have attempted to determine the prey preference of wolves, and hence the species more heavily influenced by wolf population dynamics (Nowak et al. 2005; Eggerman et al. 2011; Wagner et al. 2012). Wolf preferential consumption of wild ungulates, and especially of wild boar, has been reported in some regions of Europe (Garzón-Heydt 1991; Rosell et al. 2001; Eggerman et al. 2011; Llaneza et al. 2011; Davis et al. 2012) due to the higher abundance and availability of wild boar in the local ungulate community (e.g. Jêdrzejewski et al. 2000) and to its increasing susceptibility in winter seasons (Smietana and Klimek 1993). In NW Spain wild boar and roe deer (*Capreolus capreolus*) are the main wild prey of wolves and their consumption increases during the birthing season, probably because of the higher vulnerability of newly born animals (Cuesta et al. 1991; Fernández-Gil 2004; Markina 2005; Nores et al. 2008; Barja 2009).

In our study, independent of environmental characteristics, wolf attacks and wild boar abundance were positively associated during autumn and winter. This finding may suggest that wolves are more frequent in areas where wild boar is locally abundant in line with density-dependent food exploitation (e.g. Peckarsky et al. 2008). The strong relationship between prey and predator population dynamics can be explained by the high predation rates of wolf on juvenile wild boar (Mech 1970; Ballard et al. 1987; Salvador and Abad 1987; Jedrzejewski et al. 1992; Mattioli et al. 2004; Nores et al. 2008) bearing in mind the usual birthing period at the end of February may be supplemented by a second in autumn if conditions are favorable for boars (e.g. Ruiz-Fons et al. 2006). In contrast to our findings showing a positive association between livestock attacks and wild boar abundance, some researchers indicate that attacks on livestock are less frequent in areas where there are high densities of several wild species for wolf to prey on (Meriggi and Lovari 1996; Urios et al. 2000; Sidorovich et al. 2003). Wolf livestock selection in this case can be explained by the encounter rate with livestock due to spatial-temporal overlap (Huggard 1993). Urios et al. (2000) found – from November to February– an increase in livestock attacks due to the increased food requirements of wolf juveniles and their first attempts to hunt easy prey. In addition, both the generalized expansion of wild ungulates and the high adaptability of wild ungulates to human-dominated landscapes have been reported as important factors which facilitate the occurrence and persistence of large predators in anthropogenic areas (e.g. Ensenrink and Vogel 2006; Basille et al. 2009; Mladenoff et al. 2009; Llaneza et al. 2011), which may enhance human-wolf conflicts.

Generalist species like wild boar show wide ecological plasticity (Saez-Royuela and Tellería 1986; Taylor et al. 1998) and this ecological trait may explain the low weight of environmental characteristics in the modulation of wild boar abundance in our models. Nevertheless, in accordance to previous knowledge on the ecology of the species, our results show that the abundance of wild boar was positively influenced by the percentage of surface occupied by mature forest (oak and beech) and heather (e.g. Acevedo et al. 2006; 2009). The wild boar likely behaved according to the food exploitation hypothesis, whereby they fed mainly on acorns in autumn and winter due to them adapting to the local and seasonal availability of food (oak acorns, beechnuts and pine needles in autumn and winter) in the Cantabrian Mountains (Santos et al. 2004; Uzal and Nores 2004). Wild boar also selected lower or medium elevation areas during the hunting season due to the absence of snow in these areas, the amount of food resources in winter time (Acevedo et al. 2006) and wild boar nest construction at the beginning of the birth peak in the final weeks of February (Fernández-Llario 2004).

Based on our findings, we suggest that the inclusion of wolf frequency alongside environmental characteristics in the models increases their ability to explain wild boar abundance and the precision of the weight assigned to each factor. Consequently, if wolf frequency was not included in the models, a slight overestimation of the weight of environmental factor may well be produced (Figure 2). Furthermore, the increase in wild boar abundance in northern Spain (e.g. Uzal and Nores 2004), requires the adoption of appropriate management strategies which pay attention to both hunting interests and natural processes. The challenge remains to determine whether controlling wildlife population effects will reduce wolf-human conflict or rather favor it, but here we provide support for a close relationship between wild boar and wolf frequency.

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References

Abaigar T, del Barrio G, Vericad J R (1994) Habitat preference of wild boar (*Sus scrofa* L., 1758) in a mediterranean environment. Indirect evaluation by signs. Mammalia 58: 201–210.

Acevedo P, Escudero MA, Muñoz R, Gortázar C (2006) Factors affecting wild boar abundance across an environmental gradient in Spain. Acta Theriol 51: 327-336.

Acevedo P, Farfán MA, Márquez AL, Delibes-Mateos M, Real R, Vargas JM (2011) Past, present and future of wild ungulates in relation to changes in land use. Landscape Ecol 26: 19-31.

Acevedo P, Quirós-Fernández F, Casal J, Vicente J (in press) Spatial distribution of wild boar population abundance: Basic information for spatial epidemiology and wildlife management. Ecol Indic, http://dx.doi.org/10.1016/j.ecolind.2013.09.019

Acevedo P, Vicente J, Alzaga V, Gortázar C (2009) Wild boar abundance and hunting effectiveness in Atlantic Spain: environmental constraints. Galemys 21: 13-29.

Acevedo P, Vicente J, Höfle U, Cassinello J, Ruiz-Fons F, Gortázar C (2007) Estimation of wild boar relative abundance and aggregation: a novel method in epidemiological risk assessment. Epidemiol Infect 135: 519-527.

Akaike H (1974) A new look at the statistical model identification. IEEE Transactions on Automatic Control 19: 716-723.

Alexandre AS, Candido AT, Petrucci-Fonseca F (2000) A população lupina Portuguesa a sul do Rio Douro. Galemys 12: 113-122.

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

Ballard WB, Whitman JS, Gardner CL (1987) Ecology of an exploited wolf population in south-central Alaska. Wildl Monogr 98: 1–54.

Barbosa AM, Brown JA, Real R (2013) modEvA: an R package for model evaluation and analysis. Beta version, available upon request.

Barja I (2009) Prey and prey-age preference by the Iberian wolf *Canis lupus signatus* in a multiple-prey ecosystem. Wildl Biol 15: 147–154.

Basille M, Herfindal I, Santin-Janin H, Linnell JDC, Odden J, Andersen R, Arild Høgda K, Gaillard J (2009) What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? Ecography 32: 683–691.

Bates D, Maechler M, Bolker B (2012) lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0. http://CRAN.R-project.org/package=lme4

Boitani L, Trapanese P, Mattei L (1995) Methods of population estimates of a hunted wild boar (*Sus scrofa* L.) population in Tuscany (Italy). J Mount Ecol 3: 204-208.

Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. Ecology 73: 1045-1055.

Burnham KP, Anderson DR (2002) Model Selection and Multi-Model Inference. New York, Springer.

Cahill S, Llimona F, Gracia J (2003) Spacing and nocturnal activity of wild boar *Sus scrofa* in a Mediterranean metropolitan park. Wildl Biol 9: 3-13.

Capitani C, Bertelli I, Varuzza P, Scandura M, Apollonio M (2004) A comparative analysis of wolf (*Canis lupus*) diet in three different Italian ecosystems. Mammal Biol 69: 1–10.

Ciucci P, Boitani L, Francisci F, Andreoli G (1997) Home range, activity and movements of a wolf pack in central Italy. J Zool Lond 243: 803‒819.

Cuesta L, Bárcena F, Palacios F, Reig S (1991) The trophic ecology of the Iberian wolf (*Canis lupus signatus* Cabrera, 1907). A new analysis of stomach’s data. Mammalia 55: 239–254.

Davis ML, Stephens PA, Willis SG, Bassi E, Marcon A, et al. (2012) Prey Selection by an Apex Predator: The Importance of Sampling Uncertainty. PLoS ONE 7(10): e47894. doi:10.1371/journal.pone.0047894

Dos Santos Reis ML, López MC (1997) Predacao de lobo ibérico (*Canis lupus signatus Cabrera, 1907*) sobre gado domestico no macico da Gralheira entre 1992-1997 Pp. 59 En: Resúmenes Situación y Conservación de las poblaciones de lobo en la Península Ibérica. SECEM, GRUPO LOBO, ASDEN, Soria.

Eggermann J, Ferrao da Costa G, Guerra AM, Kirchner WH, Petrucci-Fonseca F (2011) Presence of Iberian wolf (*Canis lupus signatus*) in relation to land cover, livestock and human influence in Portugal. Mammal Biol 76: 217–221.

Engeman RM, Massei G, Sage M, Gentle MN (2013) Monitoring wild pig populations: a review of methods. Environ Sci Pollut Res. DOI 10.1007/s11356-013-2002-5

Ensenrink M, Vogel G (2006) The carnivore comeback. Science 314: 746–749.

Fernández-Gil A (2004) Sobre los hábitos alimenticios en la Cordillera Cantábrica del lobo (*Canis lupus*). Locustella 2, 24-37.

Fernández-Llario P (2004) Environmental correlates of nest site selection by wild boar *Sus scrofa*. Acta Theriol 49: 383-392.

Fonseca C, Alves da Silva A, Alves J, Vingada J, Soares A MVM (2011) Reproductive performance of wild boar females in Portugal. Eur J Wildl Res 57:363–371

Fritts SH, Mech LD (1981) Dynamics, movement and feeding ecology of a newly protected wolf population in Northwestern Minnesota. Wildl Monogr 80: 3–79.

Garzón-Heydt P (1991) Biology and ecology of wild boar (*Sus scrofa* L., 1758) in Monfragüe Natural Park. PhD Thesis, Universidad Autónoma de Madrid.

Gazzola A, Bertelli I, Avanzinelli E, Tolosano A, Bertotto P, Apollonio M (2005) Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. J Zool Lond 266: 205–213.

Gerard JF, Teillaud P, Spitz F, Mauguet R, Campan R (1991) Le sanglier. - Revue d’Ecologie (Terre Vie) 6: 11-66.

Glasser JW (1982) A theory of trophic strategies: the evolution of facultative specialists. Ecology 63: 250-262.

Gortázar C, Herrero J, Villafuerte R, Marco J (2000) Historical examination of the status of large mammals in Aragon, Spain. Mammalia 64: 411–422.

Herrero J, García-Serrano A, Couto S, Ortuño VM, García-González R (2006) Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. Eur J Wildl Res 52: 245-250.

Hosseini-Zavarei F, Farhadinia MS, Beheshti-Zavareh M, Abdoli A (2013) Predation by grey wolf on wild ungulates and livestock in central Iran. J Zool 290: 127–134.

Huggard DJ (1993) Prey selectivity of wolves in Banff National Park. I. Prey species. Can J Zool 71: 130-139.

Imperio S, Ferrante M, Grignetti A, Santini G, Focardi S (2010) Investigating population dynamics in ungulates: Do hunting statistics make up a good index of population abundance? Wildl Biol 16: 205-214.

Jedrzejewski W, Jedrzejewska B, Okarma H, Ruprecht L (1992) Wolf predation and snow cover as mortality factors in the ungulate community of the Białowieza National Park, Poland. Oecologia 90: 27-36.

Jedrzejewski W, Schmidt K, Theuerkauf J, Jedrzejewska B, Okarma H (2000) Prey selection and predation by wolves in Biolwieza Primeval Forest, Poland. J Mammal 81: 197–212.

Jedrzejewski W, Schmidt K, Theuerkauf J, Jedrzejewska B, Okarma H (2002) Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Białowieza primeval forest in Poland. Can J Zool 79:1993‒2004

Jhala YV (1993) Predation on blackbuck by wolves in Velavadar National Park, Gujarat, India. Conser Biol 7: 874-881.

Kanzaki N, Perzanowski K, Nowosad M (1998) Factors affecting wild boar (*Sus scrofa*) population dynamics in Bieszczady, Poland. Gibier Faune Sauvage 15: 1171-1178.

Keuling O, Baubet E, Duscher A, Ebert C, Fischer C, Monaco A, Podgórski T, Prevot C, Ronnenberg K, Sodeikat G, Stier N, Thurfjell H (2013) Mortality rates of wild boar *Sus scrofa L.* in central Europe. Eur J Wildl Res DOI 10.1007/s10344-013-0733-8

Kronmal RA (1993) Spurious Correlation and the Fallacy of the Ratio Standard Revisited. Journal of the Royal Statistical Society. Series A (Statistics in Society) 156: 379-392.

Kusak J, Majic´ Skrbins A, Huber D (2005) Home ranges, movements, and activity of wolves (*Canis lupus*) in the Dalmatian part of Dinarids, Croatia. Eur J Wildl Res 51: 254‒262

Latham J (1999) Interspecific interactions of ungulates in European forests: an overview. For Ecol Manage 120: 13-21.

Llaneza L, López-Bao JV, Sazatornil V (2011) Insights into wolf presence in human dominated landscapes: the relative role of food availability, humans and landscape attributes. Diversity Distrib 18: 459–469.

Llaneza L, Rico M, Iglesias J (1998) Descripción y resultados de varios métodos de muestreo para la detección y censo de lobo ibérico (*Canis lupus signatus*) en una zona de montaña. Galemys 10: 135-149.

Markina F (2005) Situación de las principales especies presa del lobo en la C.A.P.V. Pp: 25-55. En: I Aula de Ecología del Lobo Ibérico 2004. Grupo Lobo de Euskadi/Euskadiko Otso Taldea. Vitoria-Gasteiz.

Mattioli L, Apollonio M, Lovari C, Siemoni N, Crudele G (1995) Wild boar as the main prey of wolf in an area of Northern Apennines (Italy). Ibex, J Mount Ecol 3: 212.

Mattioli L, Capitani C, Avanzinelli E, Bertelli I, Gazzola A, Apollonio M (2004) Predation by wolves (*Canis lupus*) on roe deer (*Capreolus capreolus*) in north-eastern Apennine, Italy. J Zool Lond 264: 249-258.

McGarigal K, Marks BJ (1995) FRAGSTATS: spatial analysis program for quantifying landscape structure. USDA. Forest Service General Technical Report PNW-GTR-351.

Mech LD (1970) The wolf: the ecology and behaviour of an endangered species. Natural History Press, Doubleday, New York: 1–389.

Melis C, Szafranska PA, Jedrzejewska B, Barton K (2006) Biogeographical variation in the population density of wild boar (*Sus scrofa*) in western Eurasia. J Biogeogr 33: 803-811.

Meriggi A, Lovari S (1996) A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? J Appl Ecol 33: 1561–1571.

Mladenoff D, Clayton MK, Pratt SP, Sickley TA, Wydeven AP (2009) Change in occupied wolf habitat in the northern Great Lakes region. Recovery of Gray wolves in the Great Lakes region of the United States (ed. by A.P. Wydeven, T.R.

van Deelen and AJ Heske), pp. 119–138. Springer Science and Business Media, New York.

Nores C, Llaneza L, Alvarez MA (2008). Wild boar *Sus scrofa* mortality by hunting and wolf *Canis lupus* predation: an example in northern Spain. Wildl Biol 14: 44-51

Nowak S, Mysajek RW, Jedrzejewska B (2005). Patterns of wolf *Canis lupus* predation on wild and domestic ungulates in the Western Carpathian Mountains (S Poland). Acta Theriol 50: 263–276.

Okarma H (1995) The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. Acta Theriol 40: 335-386.

Peckarsky BL, Abrams PA, Bolnick DI, Dill LM, Grabowski JH, Luttbeg B, Orrock JL, Peacor SD, Preisser EL, Schmitz OJ, Trussell GC (2008) Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator–prey interactions. Ecology 89: 2416–2425.

Peterson RO, Vucetich JA, Page RE, Chouinard A (2003) Temporal and spatial aspects of predator-prey dynamics. Alces 39, 215-232.

Pimenta V, Barroso I, Álvares F, Correia J, Ferrão da Costa G, Moreira L, Nascimento J, Petrucci-Fonseca F, Roque S, Santos E (2005) Situação populacional do Lobo em Portugal: resultados do censo nacional 2002/2003. Instituto da Conservação da Natureza / Grupo Lobo, Lisboa.

Rodríguez-Prieto V, Martínez-López B, Barasona JA, Acevedo P, Romero B, Rodriguez-Campos S, Gortázar C, Sánchez-Vizcaíno JM, Vicente J (2012) A Bayesian approach to study the risk variables for tuberculosis occurrence in domestic and wild ungulates in South Central Spain. BMC Vet Res 8:148.

Rosell C, Fernández-Llario P, Herrero J (2001) The wild boar (*Sus scrofa* Linnaeus, 1758). Galemys 13:1–25.

Ruiz-Fons F, Vicente J, Vidal D, Höfle U, Villanúa D, Gauss C, Segalés J, Almería S, Montoro V, Gortázar C (2006) Seroprevalence of antibodies against six reproductive pathogens in European wild boar (*Sus scrofa*) from Spain: the effect of management. Theriogenology 65: 731-743.

Saez-Royuela C, Telleria JL (1986) The increased population of the wild boar (*Sus scrofa* L.) in Europe. Mamm Rev 16: 97-101.

Salvador A, Abad PL (1987) Food habits of a wolf population (*Canis lupus*) in Leon Province, Spain. Mammalia 51: 45-52.

Santos P, Mexia de Almeida L, Petrucci- Fonseca F (2004) Habitat selection by wild boar *Sus scrofa* L. in Alentejo, Portugal. Galemys 16: 167-184.

Santos JPV, Fernández-de-Mera IG, Acevedo P, Boadella M, Fierro Y, Vicente J, Gortázar C (2013) Optimizing the sampling effort to evaluate body condition in ungulates: A case study on red deer. Ecol Indic 30: 65-71.

Schmitz OJ, Hambaeck PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. American Naturalist 155: 141-153.

Serrano E, Alpizar-Jara R, Morelett N, Hewison AJM (2008) A half a century of measuring ungulate body condition using indices: is it time for a change? Eur J Wildl Res 54: 675–680.

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

Sidorovich VE, Tikhomirova LL, Jedrzejewska B (2003) Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990-2000. Wildl Biol 9: 103-111.

Śmietana W, Klimek A (1993) Diet of wolves in the Bieszczady Mountains, Poland. Acta Theriol 38: 245-251.

Talegón J, Gayol X (2010) El uso de las estadísticas de predación sobre ganado en la gestión y conservación del lobo en la Península Ibérica. Pp. 117-135. In: A Fernández-Gil, F Alvares, C Vilá and A Ordiz (eds.). Los lobos de la Península Ibérica. Propuestas para el diagnóstico de sus poblaciones. ASCEL, Palencia.

Taylor RB, Hellgren EC, Gabor TM, Ilse LM (1998) Reproduction of feral pigs in Southern Texas. J Mammol 79:1325-1331.

Treves A, Naughton-Treves L, Harper EK, Mladenoff DJ, Rose RA, Sickley TA, Wydeven AP (2004) Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. Conserv Biol 18: 114-125.

Urios V, Vilá C, Castroviejo J (2000) Estudio de la incidencia real de la depredación del lobo en la ganadería comparando dos métodos distintos. Galemys 12: 241-248.

Uzal A, Llaneza L (2010) Análisis de la distribución en el estudio del lobo en la Península Ibérica. Pp. 21-36. In: A Fernández-Gil, F Alvares, C Vilá and A Ordiz (eds.). Los lobos de la Península Ibérica. Propuestas para el diagnóstico de sus poblaciones. ASCEL, Palencia.

Uzal A, Nores C (2004) Endogenous and exogenous constraints in the population changes of wild boar (*Sus scrofa* Linnaeus, 1758). Galemys 16: 83-98.

Valdmann H, Andersone-Lilley Z, Copa O, Ozolins J, Bagrade G (2005) Winter diets of wolf *Canis lupus* and lynx *Lynx lynx* in Estonia and Latvia. Acta Theriol 50: 521-527.

Wagner C, Holzapfel M, Kluth G, Reinhardt I, Ansorge H (2012) Wolf (*Canis lupus*) feeding habits during the first eight years of its occurrence in Germany. Mammal Biol 77:196-203.

Table 1. Results of generalized linear mixed models explaining variation in wild boar relative abundance. Only the best models (i.e. those with the lowest AIC) are shown. See Appendix 1 for the full list of models tested.

AIC: 2731

Model Predictors	Estimate	SE	Z value	P
Surface Area	0.2146	0.0583	3.675	<0.001
Period	0.0775	0.0163	4.747	<0.001
Hunting effort	0.0281	0.0074	3.786	<0.001
Elevation	-0.0005	0.0002	-1.811	<0.100
Mature forest	0.5699	0.2486	2.292	<0.050
Heather	2.1344	0.5394	3.957	<0.001
Wolf frequency	0.0678	0.0055	12.214	<0.001

AIC: 2732

Model Predictors	Estimate	SE	Z value	P
Surface Area	0.2019	0.0600	3.361	<0.001
Period	0.0771	0.1632	4.724	<0.001
Hunting effort	0.0281	0.0074	3.802	<0.001
Elevation	-0.0004	0.0002	-1.672	<0.100
Mature forest	0.6100	0.2527	2.414	<0.050
Heather	2.0988	0.5407	3.881	<0.001
Diversity	0.1157	0.1215	0.952	0.341
Wolf frequency	0.0676	0.0055	12.18	<0.001

AIC: 2732

Model Predictors	Estimate	SE	Z value	P
Surface Area	0.1886	0.0573	3.292	<0.001
Period	0.0776	0.0163	4.755	<0.001
Hunting effort	0.0274	0.0074	3.709	<0.001
Mature forest	0.4468	0.2357	1.896	<0.100
Heather	2.0284	0.5359	3.785	<0.001
Wolf frequency	0.0681	0.0055	12.259	<0.001

AIC:2733

Model Predictors	Estimate	SE	Z value	P
Surface Area	0.1925	0.0604	3.185	<0.001
Period	-0.0004	0.0003	-1.533	<0.001
Hunting effort	0.0280	0.0074	3.787	<0.001
Elevation	-0.0004	0.0003	-1.533	0.125
Mature forest	0.5937	0.2525	2.351	<0.05
Heather	2.0614	0.5402	3.816	<0.001

Diversity	0.1545	0.1287	1.200	0.230
Fern	-0.6190	0.6538	-0.947	0.344
Wolf frequency	0.0670	0.0055	12.185	<0.001

Figure captions

Figure 1. Geographical location of Asturias in Spain, location of study areas in the Cantabrian Mountains (NW Spain) and detail for one RGR and its hunting areas and drives. Polygons show Regional Game Reserves (RGRs, in bold black), hunting areas (in black) and drives (grey areas) where data on wild boar abundance were obtained and white circles show wolf attacks.

Figure 2. Variation partitioning results for the three factors retained in the most parsimonious GLMM model including surface area, period and hunting effort as hunting methodology factor; mature forest, heather and elevation as environment factor; and wolf frequency.

Figure1

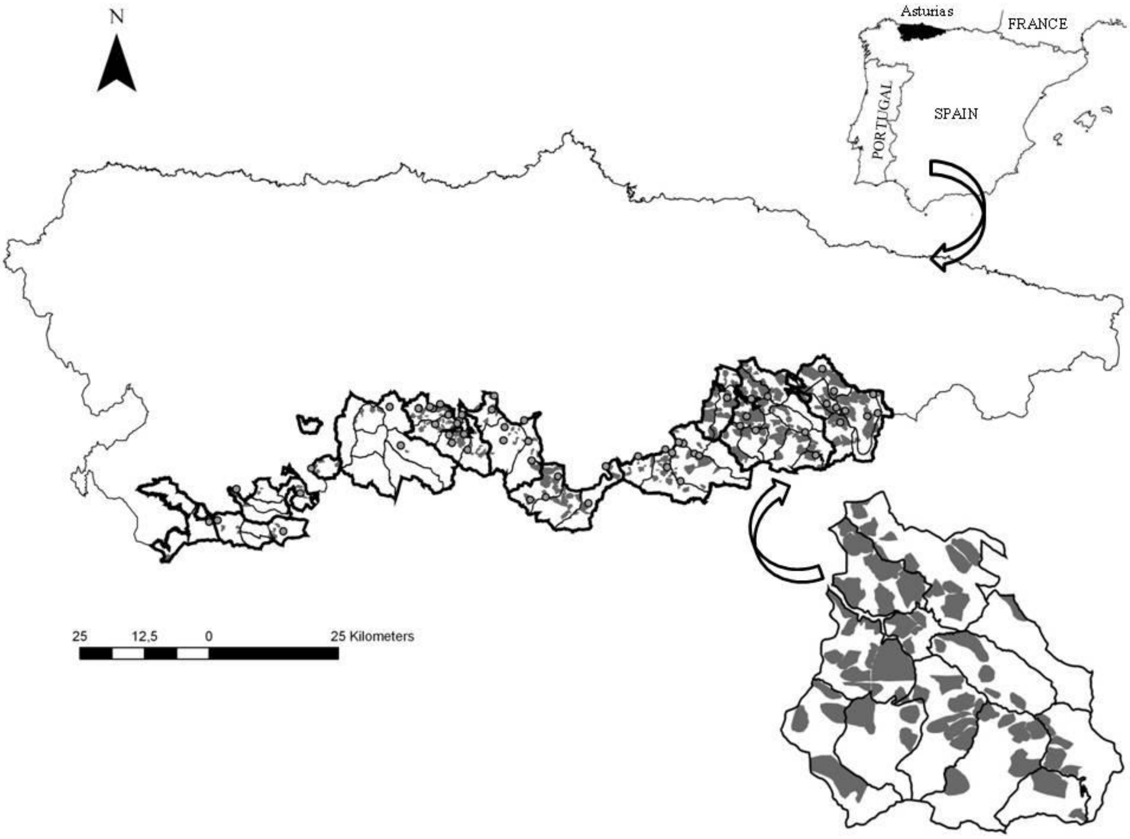
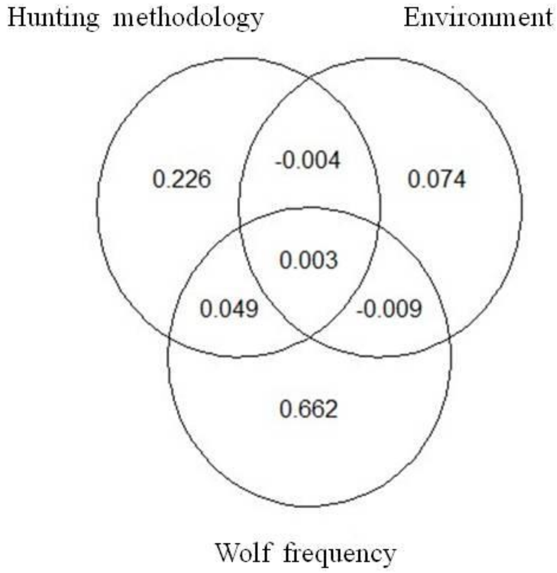


Figure 2


Hunting methodology
Environment
0.226
-0.004
0.074
0.003
0.049
-0.009
0.662
Wolf frequency

Supplementary Material

Biotic and abiotic factors modulating wild boar relative abundance in Atlantic Spain

Appendix 1**.** List of the 10 models tested per indicator group and their AIC values following a backward stepwise process. The best models (separated by less than 2 AIC points) are highlighted in bold.

A=surface area; P= period; He=hunting effort; E=elevation; S=slope; SW=southwest orientation; Mf=mature forest; H=heather; F=fern; Pr=preforest; Sh=shrub; P=tree plantation; M=meadows; D=vegetation diversity; W=wolf frequency

Variables	**AIC**
A+P+H e+E+M f+H+W	**2731**
A+P+H e+E+M F+H+D+W	**2732**
A+P+H e+MF+H+W	**2732**
A+P+H e+E+M f+H+F+D+W	**2733**
A+P+H e+E+M f+H+F+P+D+W	2734
A+P+H e+E+M f+Pr+H+F+P+D+W	2735
A+P+H e+S+E+M f+P+H+F+Ps+D+W	2737
A+P+H e+S+E+M f+Pr+H+F+P+M+D+W	2739
A+P+H e+S+E+M f+Pr+Sh+H+F+P+M+D+W	2741
A+P+H e+S+E+SW+M f+Pr+Sh+H+F+P+M+D+W	2743

Appendix 2. Variation partitioning results for the three factors resulting from the three GLMM models: A, with AIC: 2732, which includes vegetation diversity; B, with AIC: 2732, which excludes elevation; C, with AIC: 2733, which includes vegetation diversity and fern. In addition all include surface area, period and hunting effort as hunting methodology factor; mature forest, heather and elevation as environment factor; and wolf frequency.