View metadata, citation and similar papers at core.ac.uk
brought to you by CORE
provided by Revistes Catalanes amb Accés Obert

Intensive monitoring suggests population oscillations and migration in wild boar *Sus scrofa* in the Pyrenees

M. Sarasa & J.–A. Sarasa

Sarasa, M. & Sarasa, J.–A., 2013. Intensive monitoring suggests population oscillations and migration in wild boar *Sus scrofa* in the Pyrenees. *Animal Biodiversity and Conservation*, 36.1: 79–88.

Abstract

Intensive monitoring suggests population oscillations and migration in wild boar Sus scrofa *in the Pyrenees*.— As few studies have analysed local variability in populations of wild boar *Sus scrofa* in Western Europe in recent years, our understanding of ecological processes currently affecting this species is limited. To analyse questions regarding local variability in wild boar abundance, we used information from 442 traditional drive hunts monitored throughout eight hunting periods in the Pyrenees mountain range (Urdués, N Spain). Results showed temporal oscillations in abundance, and a non–linear decrease of 23% in the number of wild boar seen per drive hunt between 2004 and 2011. Numbers of dogs and hunters per drive hunt also affected indexes of wild boar abundance. Inter–annual variations in bag size may cause overestimations of variations in boar abundance and may even deviate from the population dynamics inferred from the number of wild boars seen per drive hunt. The multimodal patterns of wild boar abundance during the hunting periods suggest migrations in the Pyrenees. Our findings highlight the limitations of hunting bag statistics in wild boar. Further studies are required to guarantee information–based sustainable management of wild boar populations.

Key words: Wild boar, *Sus scrofa,* Animal migration, Big game traditional hunting, Population dynamics, Wildlife management.

Resumen

*El seguimiento intensivo sugiere la existencia de oscilaciones demográficas y movimientos migratorios en las poblaciones de jabalí (*Sus scrofa*) en los Pirineos*.— Muy pocos estudios recientes han analizado la variabilidad local de las poblaciones de jabalí (*Sus scrofa*) en Europa occidental, lo que limita nuestra comprensión de los procesos ecológicos que en la actualidad afectan a esta especie. Usando la información recopilada mediante el seguimiento de 442 batidas durante ocho temporadas de caza en los Pirineos (Urdués, norte de España), se analizaron cuestiones relacionadas con la variabilidad local de la abundancia de jabalí. Los resultados revelaron oscilaciones temporales de la abundancia y una disminución discontinua del 23% en el número de jabalíes avistados por batida entre 2004 y 2011. El número de perros y de cazadores por batida también afectó a los índices de abundancia de jabalí. Las variaciones interanuales de animales abatidos pueden provocar que se sobreestimen las variaciones de la abundancia de jabalí e incluso pueden desviarse de la dinámica de poblaciones inferida del número de jabalíes avistados por batida. En los Pirineos, el patrón multimodal de la abundancia de jabalí durante las temporadas de caza sugiere la existencia de movimientos migratorios. Los resultados obtenidos destacan las limitaciones de las estadísticas de abundancia realizadas sobre el número de jabalíes abatidos y ponen de manifiesto la necesidad de llevar a cabo nuevos estudios que permitan gestionar las poblaciones de jabalí de forma sostenible y fundamentada.

Palabras clave: Jabalí, *Sus scrofa*, Migración, Caza mayor tradicional, Dinámica de poblaciones, Gestión de la fauna silvestre.

Received: 13 I 13; Conditional acceptance: 3 III 13; Final acceptance: 22 III 13

Mathieu Sarasa, Grupo Biología de las Especies Cinegéticas y Plagas (RNM–118), España (Spain).– Juan–Antonio Sarasa, Grupo de Caza Mayor de Urdués, España (Spain).

Corresponding author: M. Sarasa, Fédération Nationale des Chasseurs 13, Rue du Général Leclerc, F–92136 Issy les Moulineaux Cedex, France. E–mail: mathieusar@hotmail.com; msarasa@chasseurdefrance.com

ISSN paper: 1578–665 X
ISSN digital: 2014–928 X

© 2013 Museu de Ciències Naturals de Barcelona

Introduction

Over the last 30 years, most studies discussing or mentioning wild boar *Sus scrofa* abundance and densities in Western Europe have suggested that overall wild boar populations are increasing (Sáez–Royuela & Tellería, 1986; Melis et al., 2006; Marco et al., 2011). Wild boar populations have been associated with health problems in livestock and humans (Artois et al., 2002; Rossi et al., 2005; Meng et al., 2009), damage to crops and colonized ecosystems (Schley et al., 2008; Cuevas et al., 2010), and road accidents (Groot Bruinderink & Hazebroek, 1996; Lagos et al., 2012). It has also been suggested that wild boar might reduce the availability of summer grazing areas through soil disturbance (Bueno et al., 2010), although such issues have raised considerable controversy (Risch et al., 2010; Wirthner et al., 2011; Wirthner et al., 2012). In light of these concerns and of the predicted increase in wild boar populations as a response to global warming (Melis et al., 2006), management tools to control and reduce wild boar populations are of much interest (Massei et al., 2011). In recent years, however, few studies of wild boar population dynamics in Western Europe have been performed (Marco et al., 2011), limiting our understanding of current ecological processes in this species.

Generalized increases in wild boar densities are thought to be responsible for increasing presence of wild boar in agricultural ecosystems and even in urban environments (Jansen et al., 2007). However, very few studies have addressed whether these increases are the result of a source–sink gradient, sustained by woodland environments with increasing numbers of wild boars, or whether wild boars are locally adapting to agricultural and urban environments in which effective and perceived hunting pressure is low and opportunist foraging is facilitated by city dwellers (Cahill & Llimona, 2004).

Increasing interest is also being shown in the way in which wild boar use space, and a number of studies have revealed variable and complex movement patterns (Keuling et al., 2010). Whilst some authors suggest that wild boars are essentially sedentary animals (Saunders & Kay, 1996; Keuling et al., 2008; Mitchell et al., 2009), others indicate that wild boars might perform sex–specific habitat selection depending on their landscape of fear (Saïd et al., 2012) or even on local migrations (Andrzejewski & Jezierski, 1978; Singer et al., 1981; D'Andrea et al., 1995).

The essential parameters regarding population dynamics and space use in wild boar are therefore unclear, thus hindering the establishment of appropriate management practices.

In this study, we used hunting data collected over eight hunting periods in a locality of the Pyrenean mountain range (Urdués, N Spain) to analyse the population dynamics and space use in the wild boar. Historically, the Pyrenees have always been considered a propitious environment for this game species (Gortázar et al., 2000). Thus, if the increase in wild boar in agricultural and urban environments is the product of a source–sink gradient sustained by woodland environments, we would expect a positive population trend at our study site during the monitoring period (prediction 1). Given the overall increase in wild boar populations referred to in other studies (Sáez–Royuela & Tellería, 1986; Marco et al., 2011), we would also expect an increase in wild boar populations in the Pyrenees (prediction 1)

Secondly, we investigated the spatial ecology of wild boar by testing two mutually exclusive hypotheses. If the wild boar is a sedentary species (hypothesis 1), we would expect a decrease in wild boar abundance in our study site during the hunting period due to the population reduction caused by hunting pressure (prediction 2). Nevertheless, if the wild boar is migratory in the Pyrenees (hypothesis 2), we would expect to observe a pattern of abundance that, rather than corresponding to a simple model of population decrease during the hunting period, exhibits a bell–shaped or a multi–modal pattern of abundance indexes during the hunting period (prediction 3).

Thirdly, we also took into account previous studies of wild boar harvesting. Null or weak relationships were recorded between the numbers of dogs and hunters and bag size per drive hunt in Italy (Scillitani et al., 2010). Thus, we expected comparable results at our study site (prediction 4).

Material and methods

Study site

We analysed local wild boar abundance on the southern side of the Pyrenees (Hecho valley, Aragón, northern Spain). This area is characterized by extensive woodlands (mainly *Pinus sylvestris*, *Fagus sylvatica* and *Quercus sspp.*) and few open habitats (Acevedo et al., 2006). Human population density is low and traditional agricultural practices are mostly focused on animal husbandry (cows, sheep, goats, and horses). In the Pyrenees, local agriculture has been changing in recent decades and the natural reforestation of former open areas has led to a loss of diversity in the landscape mosaic (Ortigosa et al., 1990; García–Ruiz et al., 1996; Roura–Pascual et al., 2005). In this area, traditional hunting drives for wild boar are conducted by one or more beaters on foot with dogs and with hunters on stands. Despite apparent intensive harvesting, the global hunting pressure on the species in the region might be low, due to the abundance of shelter areas (Acevedo et al., 2006; Herrero et al., 2008). In this study we monitored the hunting group from the village of Urdués, which harvests wild boar in their local area (25 km^2). In this study, the moderate scale of the area and the detailed information of our data set allowed a more precise monitoring of the local abundance of wild boar than in previous studies on wild boar in Aragón (detailed thereafter).

Data collection

Close collaboration with hunters allowed us to generate a database that included details of the drive hunts that were not included in previous studies on wild boar. Although reliable estimates of ungulate abundance can be made when the numbers of individuals seen on hunts are available (Ericsson & Wallin, 1999; Mysterud et al., 2007; Rönnegård et al., 2008), this information has rarely been available in previous studies on wild boars (Sáez–Royuela & Tellería, 1988; Tellería, 2004). Hunting statistics could also act as a good index of wild boar population abundance (Tellería, 2004; Imperio et al., 2010), even though official hunting statistics in Spain are incomplete and of questionable accuracy (Martínez–Jaúregui et al., 2011). We monitored the number of wild boars seen and culled during each drive hunt. The area in which the hunt took place and the number of dogs and hunters were also recorded. In total, data from 442 drive hunts were recorded during hunting periods (2.21 drive hunts per km^2 per hunting period) from 2004 to 2012. For this study our monitoring allowed a fine–resolution that is close to forty times greater than those of previous studies on wild boar in this region (2,657 drive hunts per hunting period for 47,669 km^2 in Aragón means close to 0.06 drive hunt per season per km^2 [Acevedo et al., 2006]). This underlines the difference of resolution between the data used in previous studies on wild boar in Aragón and the data set used in this study.

Analysis

We considered two indexes of wild boar abundance: the number of wild boars seen (index 1) and the number of wild boars culled (index 2) per drive hunt. To analyse the determining factors in these indexes of abundance, we used General Additive Models (GAMs) (Wood, 2006; Zuur et al., 2007). The explanatory variables considered were: (Y) the year in which the hunting period started; (D) the day of the hunting period: for the first day of each hunting period, we used the day number according to the Gregorian calendar and then added the number of days up to the end of the hunting period; (Nd) the number of dogs; (Nh) the number of hunters. In the Pyrenees, the number of hunters per drive hunt in traditional hunting groups (mean ± SE = 7 ± 2.8) rarely or never allows coverage of all the potential escape routes of the hunted patch. Also, data concerning the exact surface hunted by beaters and dogs (mean number of dogs per drive hunt ± SE = 9.8 ± 3.6) is usually unavailable because the courses of the dogs are not systematically recorded with telemetric tools. The exact hunted area is thus usually unknown. In this study, the approximate area potentially hunted during each drive hunt was close to 2.5 km^2. Furthermore, instead of using estimated surfaces characterized by overblown and unreliable accuracy, we tested the area in which the drive hunt took place as a potential co–factor to account for the potential effects of spatial heterogeneity on wild boar abundance.

We used an information–theoretic approach based on the Akaike's information criterion corrected for a small sample size (AICc; Burnham & Anderson, 2002). The analysis identified the most parsimonious model (lowest AICc) of possible subsets, ranging from the null model (MO, intercept only) to a model with all the considered explanatory variables. This analytical procedure selects the model that provides an accurate approximation to the structural information in the data at hand, with the smallest possible number of parameters for adequate representation of the data (Burnham & Anderson, 2002). The Akaike weight of models (Wi) was presented —the weight of evidence in favour of the considered model being the best model for the situation at hand (Burnham & Anderson, 2002). The relative importance (RI) of the explanatory variables was estimated —by the sum of the Akaike weights over all models in which that variable appears– to highlight evidence for the importance of each variable within the set of models (Burnham & Anderson, 2002). Explained deviance values (Dev–expl), providing an estimate of the model fit (Wood, 2006), are also presented. All analyses were performed using the R statistical software (R Development Core Team, 2011).

Results

Variability in wild boar abundance indexes depended on temporal factors —the hunting period and the day in the hunting period— and on the characteristics of the drive hunt —the number of dogs and hunters and the area. Model selection suggests for both wild boars seen and wild boars culled that the best model for the data at hand includes as explanatory factors the year, the day of the season, the interaction between these two factors, the number of dogs and hunters, and the area (table 1 and 2). Over the considered period, the numbers of wild boars seen and culled per drive hunt showed non–linear trends (fig. 1). For the number of wild boars seen per drive hunt, the fitted model suggests an increase of 13% between 2004 and 2005, a decrease of 44% between 2005 and 2009, and an increase of 20% between 2009 and 2011. Between 2004 and 2011, this model suggests an overall reduction of 23% in the number of wild boars seen per drive hunt (fig. 1A, left). For the number of wild boars culled per drive hunt, the selected model suggests an oscillatory pattern with substantial increases (101% between 2004 and 2005; 57% between 2007 and 2008) and decreases (–46% between 2005 and 2007; –66% between 2008 and 2010). Between 2004 and 2011, this model suggests a 14% increase in the number of wild boars culled per drive hunt (fig. 1B, left). These inter–annual trends interact with a multimodal pattern that exhibits variations depending on the hunting period (fig. 2A).

The number of wild boars seen per drive hunt was highest at the beginning of the hunting period (early October), in early January, and in February in 2004–2006. However, this pattern changed over the study period and the number of wild boars seen was highest in December and February in 2006–2009. Since 2009, however, the periods with greatest numbers of wild boars seen were the same as in previous years but with the difference that the peaks of abundances in boar seen decreased in comparison with the period 2004–2009 (fig. 2A, left). The number of wild boars seen per drive hunt was positively associated with the number of hunters (at least up to ten hunters) (fig. 2B, left) and also increased strongly in drive hunts with 10–18 dogs (fig. 2B, left). A decrease in the number of wild boar

Table 1. Model selection for determining factors in the number of wild boar *Sus scrofa* seen per drive hunt: Y. Hunting period; D. Day of the hunting period; Nd. Number of dogs; Nh. Number of hunters; A. Area where the drive hunt took place; * interaction; *K*. Number of estimated parameters; AICc. Akaike's Information Criterion corrected for small sample size, lower values indicate a most–parsimonious model for the observed data; ΔAICc. Difference of AICc between the model and the most parsimonious model; the larger the ΔAICc, the less plausible it is that the fitted model is the best model given the data set; L(gi/x). Probability of the model being the best model given the data set; Wi. Akaike weight of the model; Dev–expl. Explained deviance of the fitted model; RI. Relative Importance of factors. Only the ten best models are reported (Burnham & Anderson, 2002; Wood, 2006).

*Tabla 1. Selección de modelos para determinar los factores que condicionan el número de jabalíes (*Sus scrofa*) avistados por batida: Y. Temporada de caza; D. Día de la temporada de caza; Nd. Número de perros; Nh. Número de cazadores; A. Área en la que tuvo lugar la batida; * Interacción;* K. *Número de parámetros estimados; AICc. Criterio de información de Akaike corregido para un tamaño muestral pequeño, los valores bajos indican un modelo principalmente parsimonioso para los datos observados; ΔAICc. Diferencia de AICc entre el modelo y el modelo más parsimonioso, cuánto mayor sea ΔAICc, menos plausible será que el modelo ajustado sea el mejor para el conjunto de datos; L(gi/x). Probabilidad de que el modelo sea el mejor para el conjunto de datos; Wi. Peso de Akaike del modelo; Dev–expl. Variabilidad explicacada del modelo ajustado; RI. Importancia relativa de los factores. Solo se muestran los diez modelos mejores (Burnham & Anderson, 2002; Wood, 2006).*

Model	*K*	AICc	ΔAICc	L(gi/x)	Wi	Dev–expl	RI	
Y+D+Y*D+Nd+Nh+A	55	1490.79	0.00	1.00	0.87	0.30	Y	1.00
Y+D+Y*D+Nd+A	48	1494.59	3.80	0.15	0.13	0.28	D	1.00
Y+D+Y*D+Nh+A	50	1509.94	19.15	0.00	0.00	0.28	Y*D	1.00
Y+D+Nd+Nh+A	34	1540.89	50.10	0.00	0.00	0.21	Nd	1.00
Y+D+Y*D+Nd+Nh	46	1548.35	57.56	0.00	0.00	0.25	Nh	0.87
D+Nd+A	21	1558.53	67.74	0.00	0.00	0.17	A	1.00
Y+D+Nh+A	29	1559.72	68.93	0.00	0.00	0.19		
Y+D+Nd+A	22	1560.71	69.92	0.00	0.00	0.17		
Y+Nd+A	14	1564.63	73.84	0.00	0.00	0.15		
D+Nh+A	25	1567.45	76.65	0.00	0.00	0.17		

seen was observed in drive hunts with more than 18 dogs, although this variation should be considered with caution due to its small sample size.

The number of wild boar culled per drive hunt revealed three key periods in the hunting periods, above all in the periods 2004–2005, 2007–2009, and 2011–2012 (fig. 2A, right): the end of December–early January and February, both characterized by the greatest number of wild boar culled per drive hunt, and lastly, the beginning of the hunting period (although the number of wild boars culled per drive hunt in this period was lower than in the other two periods). The number of wild boars culled per drive hunt also increased with the numbers of hunters and dogs, above all in drive hunts with 12–18 dogs (fig. 2B, right).

All the considered factors have very high relative importance (close to 1) in explaining the variability in the indexes of wild boar abundance (table 1 and 2). Yet, the explained deviance of the selected models was moderate (30% for wild boar seen and 23% for wild boar culled), which suggests that the considered factors only provide a partial understanding of the observed variability.

Discussion

Multimodal patterns in wild boar abundance indexes during hunting periods suggest that wild boar conduct seasonal migrations in our study site. Migrations are a more likely explanation than nomadism (Mueller & Fagan, 2008) because the environment is highly seasonal in the Pyrenees and because pulsations in wild boar abundance during the hunting period occur over years and in certain predictable times of the hunting period. The boar mating season at the end of December–early January (Delcroix et al., 1990), for instance, is one of the periods when high abundances of wild boar are most predictable. Thus, the observed variations in wild boar abundance may be linked —at least in part— to the behavioural ecology of the species in the area. The observed evidence of wild boar migrations in our area differs from the sedentary patterns reported in Germany and Australia (Keuling et al., 2008; Mitchell et al., 2009) but agrees with results from Poland and mountainous environments in Italy and in Tennessee, USA (Andrzejewski & Jezierski, 1978; Singer et al., 1981; D'Andrea et al., 1995). Patterns in the use of

Table 2. Model selection for determining factors in the number of wild boar *Sus scrofa* culled per drive hunt. Only the ten best models are reported. (Burnham & Anderson, 2002; Wood, 2006). (For abbreviations see table 1.)

Tabla 2. Selección de modelos para determinar los factores que condicionan el número de jabalíes Sus scrofa *abatidos por batida. Solo se han mostrado los diez modelos mejores (Burnham & Anderson, 2002; Wood, 2006). (Para las abreviaturas, ver tabla 1.)*

Model	*K*	AICc	ΔAICc	L(gi/x)	Wi	Dev–expl	RI	
Y+D+Y*D+Nd+Nh+A	26	758.41	0.00	1.00	0.94	0.23	Y	0.98
D+Nd+A	18	766.03	7.62	0.02	0.02	0.18	D	0.98
Y+Nd+A	14	767.11	8.70	0.01	0.01	0.16	Y*D	0.95
Y+D+Y*D+Nd+A	20	767.60	9.19	0.01	0.01	0.19	Nd	0.99
Y+D+Nd+A	19	767.84	9.43	0.01	0.01	0.18	Nh	0.95
Y+D+Nd+Nh+A	20	769.77	11.36	0.00	0.00	0.18	A	1.00
Y+D+Y*D+Nh+A	23	772.44	14.03	0.00	0.00	0.19		
Y+D+Nh+A	22	772.94	14.53	0.00	0.00	0.19		
Y+Nh+A	17	774.60	16.19	0.00	0.00	0.16		
Y+D+Y*D+Nd+Nh	18	782.29	23.88	0.00	0.00	0.17		

space in wild boar, therefore, appear to be highly dependent on the environment. As in other European ungulates (Albon & Langvatn, 1992; Mysterud, 1999; Ball et al., 2001) and as previously suggested for the wild boar (Andrzejewski & Jezierski, 1978), migrations may involve only part of the wild boar population (partial migration) and still require further study. The knowledge of wild boar migration in the Pyrenees may stimulate a reappraisal of significant variations in local populations. The sustainable management of migratory species requires an accurate understanding and familiarity with migratory routes (Thirgood et al., 2004; Bolger et al., 2008), and such knowledge would represent a substantial challenge for future management plans. Further studies should aim to characterize the life–history, the spatial scale, the phenology and the determining factors of migration (Ramenofsky & Wingfield, 2007) of wild boar in the Pyrenees. Previous studies on space use in wild boar suggested small home ranges at small time scales (< 1,000 ha in average; Massei et al., 1997; Keuling et al., 2008). The choice of temporal scale at which data are collected and the definition of home range can significantly influence biological inference (Börger et al., 2006). The size of our study site (2,500 ha) and our intense monitoring were key factors that allowed us to reach high–resolution analyses of variations in wild boar abundance. Further studies should use movement data at small temporal scale and take into account reproductive ecology and food availability, not just hunting period. Integrated and high–resolution monitoring is required to unravel the misunderstood complexity of space use in wild boar.

The number of wild boar seen and culled per drive hunt varied substantially during the monitoring period and the trends in these two abundance indexes differed. Inter–annual variations were greater for wild boars culled than for wild boars seen per drive hunt and on occasions the trends in abundance for each index were different. For instance, in the period 2004–2011, the results for the wild boars seen per drive hunt suggest a reduction of 23%, while the results for wild boars culled per drive hunt suggest an increase of 14%. The number of wild boars seen per drive hunt is probably a more reliable index of wild boar abundance than the number of wild boars culled because it is not dependent on shooting success and because indexes based on seen–individuals have previously been preferred in other ungulate species (Ericsson & Wallin, 1999; Mysterud et al., 2007). Variations in the migratory/resident ratio might also affect the relationship between the numbers of wild boar seen and culled through dilution effects on predation risk (Krause & Ruxton, 2002). Thus, strong inter–annual variations in the number of culled wild boar should be regarded with caution as this abundance index might overestimate or even deviate from true population dynamics. Further studies are required to unravel the relative importance of shooting success.

As seen above, the number of wild boars seen per drive hunt suggests a non–linear decrease of 23% in 2004–2011 in our study site. Indirect evidence of wild boar migration were observed and, therefore, further studies should analyse the spatial scale of this decreasing population trend. The population dynamics of wild boar in other areas should also be examined using indexes other than hunting bag alone. The observed inter–annual pattern disagrees with the results reported by Marco et al. (2011) that suggest —on the basis of official hunting statistics and for an area that included

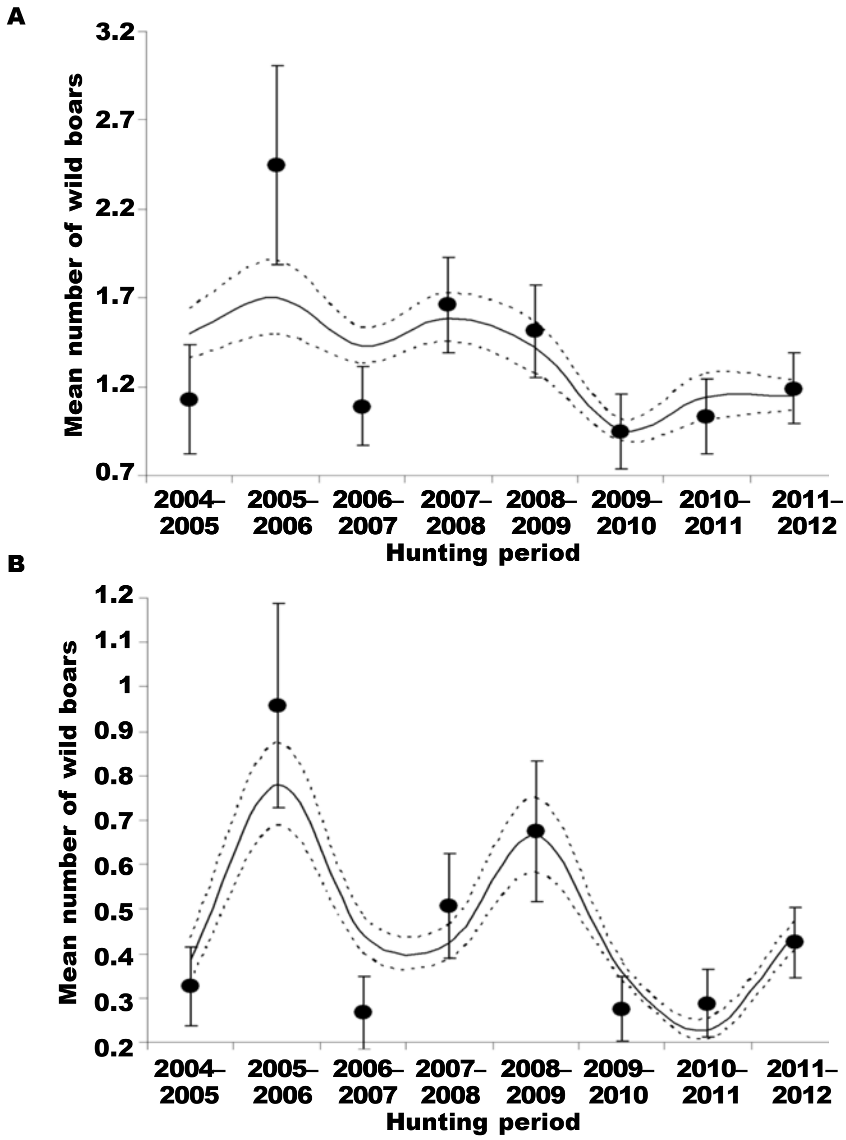

Fig. 1. Inter–annual variation in the indexes of wild boar abundance in Urdués (Pyrenees, northern Spain): A. Number of wild boars seen per drive hunt; B. Number of wild boars culled per drive hunt. Points and error bars represent mean values and related standard error. The solid lines represent the predicted patterns estimated by the best models and the dotted lines indicate the related standard error.

Fig. 1. Variación interanual en los índices de abundancia de jabalí en Urdués (Pirineos, norte de España): A. Número de jabalíes avistados por batida; B. Número de jabalíes abatidos por batida. Los puntos y las barras de error representan los valores medios y el error estándar relacionado. Las líneas continuas representan los patrones previstos estimados con los mejores modelos y las discontinuas indican el error estándar relacionado.

our study site— that wild boar populations increased in Aragón during this period. This incongruence might be caused by differences in the spatial scale considered. Nevertheless, as highlighted by Martínez–Jauregui et al. (2011), in Spain official hunting statistics can be incomplete and thus this discrepancy may be due to differences in the accuracy and in the completeness of the available information. Between 1997 and 2002, Acevedo et al. (2006) suggested a population increase in the Pyrenees (woodland habitat) and relative population stability or local decrease in central and south Aragón (which is characterized by a more developed agriculture than the Pyrenees). This might suggest that wild boar population dynamics might have changed in

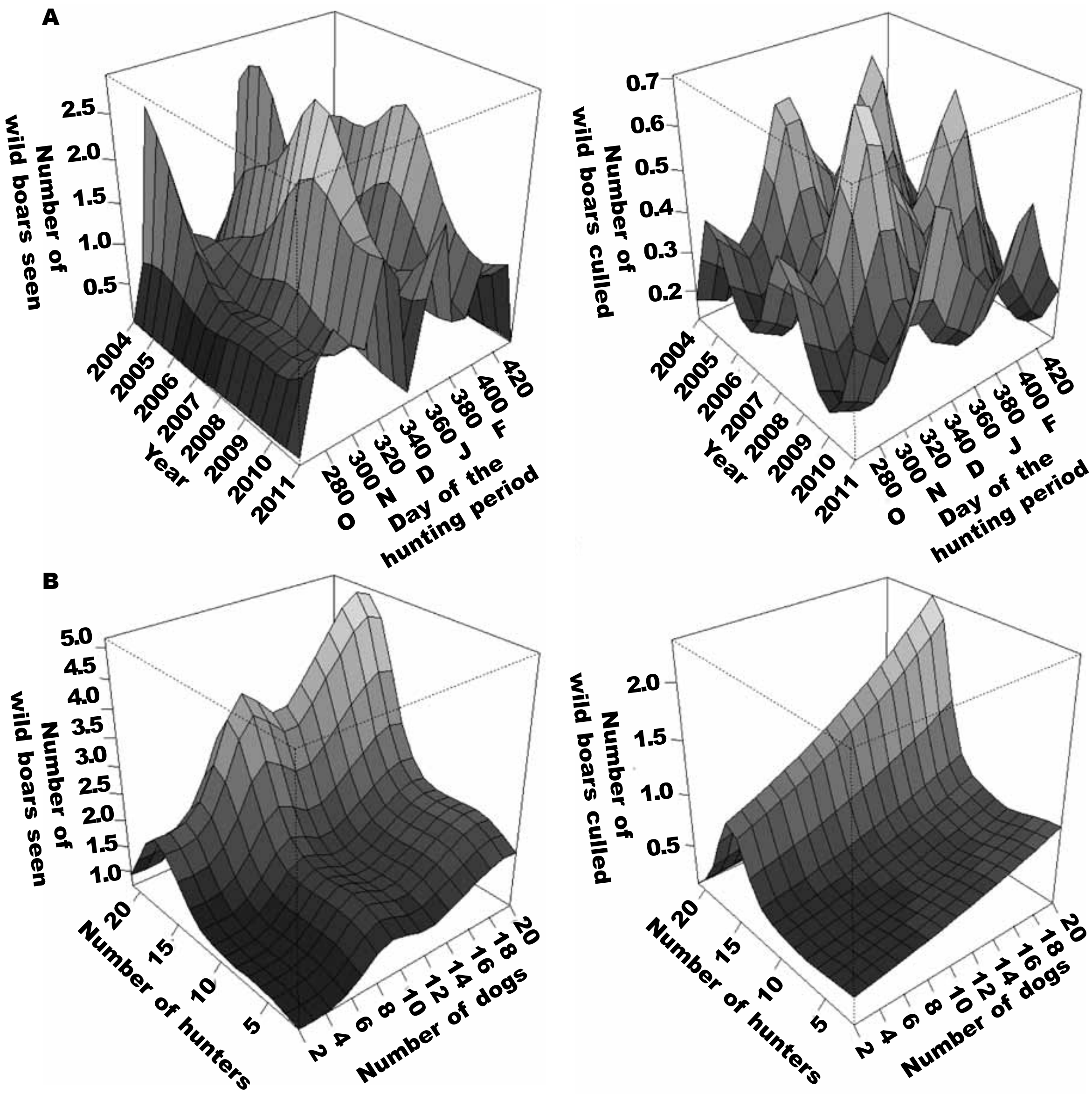

Fig. 2. Determining factors in the number of wild boar seen (left) and number of wild boar culled (right) per drive hunt: A. Effect of year and day of the hunting period (O. October; N. November; D. December; J. January; F. February); B. Effects of the numbers of dogs and hunters.

Fig. 2. Factores determinantes en el número de jabalíes avistados (izquierda) y número de jabalíes abatidos (derecha) por batida: A. Efecto del año y el día de la temporada de caza (O. Octubre; N. Noviembre; D. Diciembre; J. Enero; F. Febrero); B. Efectos del número de perros y de cazadores.

the Pyrenees, at least locally. However, this interpretation should be considered with caution because the results of Acevedo et al. (2006) were based on hunting bag size and their study had a much lower resolution than ours. We showed that inter–annual variations in bag size may deviate from the population dynamics inferred from the number of wild boars seen per drive hunt and, thus, results of previous studies should be considered with caution.

In Aragón, as in other European regions, wild boar can be hunted with no limit on bag size and the assumed population increase may have led authorities to advance the hunting period by two weeks since 2009 (Boletín Oficial de Aragón, 2008, 2009). Variations in wild boar abundance indexes observed during this study question the accuracy of the fine–tuning from one year to the next of the management of wild boar in Aragón. As in wild boar populations in Eastern Europe

(Danilov & Panchenko, 2012), wild boar populations in Western Europe oscillate —both increases and reductions occur— and this could be taken into account in further management plans. As for other game species, the sustainability of harvested wild boar populations —as a limited natural resource— will depend on the integration of results such as those we present here into future management plans to avoid population collapse (Fryxell et al., 2010). Past examples in Italy, Russia, Scandinavia and the United Kingdom already showed that severe population declines in wild boar or even a collapse were possible when the environmental conditions became too adverse (Apollonio et al., 1988; Leaper et al., 1999; Welander, 2000; Rosvold et al., 2010; Danilov & Panchenko, 2012). Thus, further studies are required to unravel the relative importance of down regulation (fructification, agricultural practices), characteristics of wild boar population (demographic structure, genetics) and of top regulation (pathogens, predators and hunting) in population dynamics of wild boar (*e.g.*, Massolo & Mazzoni della Stella, 2006; Rosell et al., 2012).

Wild boar population dynamics at our study site does not support the hypothesis of a generalized increase in wild boar densities in woodland areas as the origin of the increasing presence of wild boars in urban environments (Jansen et al., 2007). The hypothesis suggesting that the species might be locally adapting to agricultural and urban environments —where hunting pressure is low and where opportunist foraging might even be facilitated by city dwellers (Cahill & Llimona, 2004)— should be analyzed more closely. Such an adaptation has already been observed in wild boar by other authors (Cahill et al., 2012; Rosell et al., 2012) and the importance of areas where hunting was banned in explaining crop damage was also highlighted (Amici et al., 2012).

In conclusion, as a result of the close collaboration with local hunters, our study was able to reveal that wild boar seen per drive hunt decreased by 23% in the period 2004–2011 in our study area in the Pyrenees. The observed patterns of wild boar abundance imply the existence of wild boar migrations and further studies should analyse population dynamics of wild boar in other areas using indexes other than hunting bag alone. Our study also highlighted the fact that the numbers of dogs and hunters affect the number of wild boars seen and culled per drive hunt, and that inter–annual variations in bag size might lead to overestimates and discrepancies with population dynamics inferred from the number of wild boars seen per drive hunt. Thus, there is still a need for further studies on the spatial ecology of wild boar and on the applied ecology of wild boar if we are to move towards sustainable and information–based management of wild boar populations.

Acknowledgements

We would like to thank Julia López, Agnès Sarasa, David Sarasa and Noelia Sánchez–López for logistic support during the study period. Thanks also to all the members of the Grupo de Caza Mayor de Urdués, and above all to César López, Jesús Jiménez, Francisco López, Eduardo López, Roberto Jiménez, Pablo López and Gabriel López for their collaboration during the monitoring period. We are grateful to Michael Lockwood and Agnès Sarasa for the English revision and to Cédric Girard–Buttoz and Sylvain Losdat for valuable comments on an earlier draft of this paper. The research activities of MS are partially supported by the Plan Andaluz de Investigación Desarollo e Innovación de la Junta de Andalucía (RNM–118). This work was conducted without specific financial support and complies with current Spanish laws.

References

Acevedo, P., Escudero, M. A., Munoz, R. & Gortazar, C., 2006. Factors affecting wild boar abundance across an environmental gradient in Spain. *Acta Theriologica,* 51: 327–336. DOI: 10.1007/BF03192685.

Albon, S. D. & Langvatn, R., 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos,* 65: 502–513.

Amici, A., Serrani, F., Rossi, C. M. & Primi, R., 2012. Increase in crop damage caused by wild boar (*Sus scrofa* L.): the 'refuge effect'. *Agronomy for Sustainable Development*, 32: 683–692.

Andrzejewski, R. & Jezierski, W., 1978. Management of a wild boar population and its effects on commercial land. *Acta Theriologica,* 23: 309–339.

Apollonio, M., Randi, E. & Toso, S., 1988. The systematics of the wild boar (*Sus scrofa* L.) in Italy. *Bolletino di Zoologia,* 55: 213–221.

Artois, M., Depner, K. R., Guberti, V., Hars, J., Rossi, S. & Rutili, D., 2002. Classical swine fever (hog cholera) in wild boar in Europe. *Revue Scientifique et Technique de l'Office International des Epizooties,* 21: 287–304.

Ball, J. P., Nordengren, C. & Wallin, K., 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildlife Biology,* 7: 39–47.

Boletín Oficial de Aragón, 2008. ORDEN de 10 de junio de 2008, del Departamento de Medio Ambiente, por al que se aprueba el Plan General de Caza para la temporada 2008–2009. 15277–15286.

Boletín Oficial de Aragón, 2009. ORDEN de 11 de junio de 2009, del Departamento de Medio Ambiente, por al que se aprueba el Plan General de Caza para la temporada 2009–2010. 16253–16263.

Bolger, D. T., Newmark, W. D., Morrison, T. A. & Doak, D. F., 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters,* 11: 63–77. DOI: 10.1111/j.1461–0248.2007.01109.x.

Börger, L., Franconi, N., Ferretti, F., Meschi, F., De Michele, G., Gantz, A. & Coulson, T., 2006. An integrated approach to identify spatiotemporal and individual–level determinants of animal home range size. *The American Naturalist,* 168: 471–485.

Bueno, C. G., Barrio, I. C., García–González, R., Alados, C. L. & Gómez–García, D., 2010. Does wild boar rooting affect livestock grazing areas in alpine grasslands? *European Journal of Wildlife Research,*

56: 765–770. DOI: 10.1007/s10344–010–0372–2
Burnham, K. P. & Anderson, D. R., 2002. *Model selection and multimodel inference: a practical information–theoric approach*. 2nd edition. Springer–Verlag, New York.
Cahill, S. & Llimona, F., 2004. Demographics of a wild boar *Sus scrofa* Linnaeus, 1758 population in a metropolitan park in Barcelona. *Galemys,* 16: 37–52.
Cahill, S., Llimona, F., Cabañeros, L. & Calomardo, F., 2012. Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the Coillserola Natural Park (Barcelona) and comparison with other locations. *Animal Biodiversity and Conservation*, 35.2: 221–233.
Cuevas, M. F., Novillo, A., Campos, C., Dacar, M. A. & Ojeda, R. A., 2010. Food habits and impact of rooting behaviour of the invasive wild boar, *Sus scrofa*, in a protected area of the Monte Desert, Argentina. *Journal of Arid Environments,* 74: 1582–1585. DOI: 10.1016/j.jaridenv.2010.05.002.
D'Andrea, L., Durio, P., Perrone, A. & Pirone, S., 1995. Preliminary data of the wild boar (*Sus scrofa*) space use in mountain environment. *IBEX Journal of Mountain Ecology,* 3: 117–121.
Danilov, P. & Panchenko, D., 2012. Expansion and some ecological features of the wild boar beyond the northern boundary of its historical range in European Russia. *Russian Journal of Ecology,* 43: 45–51. DOI: 10.1134/S1067413612010043.
Delcroix, I., Mauget, R. & Signoret, J. P., 1990. Existence of synchronization of reproduction at the level of the social group of the European wild boar (*Sus scrofa*). *Journal of Reproduction and Fertility,* 89: 613–617.
Ericsson, G. & Wallin, K., 1999. Hunter observations as an index of moose *Alces alces* population parameters. *Wildlife Biology,* 5: 177–185.
Fryxell, J. M., Packer, C., McCann, K., Solberg, E. J. & Sæther, B. E., 2010. Resource management cycles and the sustainability of harvested wildlife populations. *Science,* 328: 903–906. DOI: 10.1126/science.1185802.
García–Ruiz, J. M., Lasanta, T., Ruiz–Flano, P., Ortigosa, L., White, S., González, C. & Martí, C., 1996. Land–use changes and sustainable development in mountain areas: a case study in the Spanish Pyrenees. *Landscape Ecology,* 11: 267–277.
Gortázar, C., Herrero, J., Villafuerte, R. & Marco, J., 2000. Historical examination of the status of large mammals in Aragón, Spain. *Mammalia,* 64: 411–422. DOI: 10.1515/mamm.2000.64.4.411.
Groot Bruinderink, G. W. T. A. & Hazebroek, E., 1996. Ungulate traffic collisions in Europe. *Conservation Biology,* 10: 1059–1067. DOI: 10.1046/j.1523–1739.1996.10041059.x.
Herrero, J., García–Serrano, A. & García–González, R., 2008. Reproductive and demographic parameters in two Iberian wild boar *Sus scrofa* populations. *Acta Theriologica,* 53: 355–364. DOI: 10.1007/BF03195196.
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? *Wildlife Biology,* 16: 205–214. DOI: 10.2981/08–051.
Jansen, A., Luge, E., Guerra, B., Wittschen, P., Gruber, A. D., Loddenkemper, C., Schneider, T., Lierz, M., Ehlert, D. & Appel, B., 2007. Leptospirosis in urban wild boars, Berlin, Germany. *Emerging Infectious Diseases,* 13: 739–742. DOI: 10.3201/eid1305.061302.
Keuling, O., Lauterbach, K., Stier, N. & Roth, M., 2010. Hunter feedback of individually marked wild boar *Sus scrofa* L.: dispersal and efficiency of hunting in northeastern Germany. *European Journal of Wildlife Research,* 56: 159–167. DOI: 10.1007/s10344–009–0296–x.
Keuling, O., Stier, N. & Roth, M., 2008. Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. *European Journal of Wildlife Research,* 54: 403–412. DOI: 10.1007/s10344–007–0157–4.
Krause, J. & Ruxton, G. D., 2002. *Living in Groups*. Oxford Univ. Press, Oxford.
Lagos, L., Picos, J. & Valero, E., 2012. Temporal pattern of wild ungulate–related traffic accidents in northwest Spain. *European Journal of Wildlife Research,* 58: 661–668 DOI: 10.1007/s10344–012–0614–6.
Leaper, R., Massei, G., Gorman, M. L. & Aspinall, R., 1999. The feasibility of reintroducing wild boar (*Sus scrofa*) to Scotland. *Mammal Review,* 29: 239–258. DOI: 10.1046/j.1365–2907.1999.2940239.x.
Marco, J., Herrero, J., Escudero, M. A., Fernández–Arberas, O., Ferreres, J., García–Serrano, A., Giménez–Anaya, A., Labarta, J. L., Monrabal, L. & Prada, C., 2011. Veinte años de seguimiento poblacional de ungulados silvestres de Aragón. *Pirineos,* 166: 135–153. DOI: 10.3989/Pirineos.2011.166007.
Martínez–Jauregui, M., Arenas, C. & Herruzo, A. C., 2011. Understanding long–term hunting statistics: the case of Spain (1972–2007). *Forest Systems,* 1: 139–150. DOI: 10.5424/fs/2011201–10394.
Massei, G., Genov, P. V., Staines, B. W. & Gorman, M. L., 1997. Factors influencing home range and activity of wild boar (*Sus scrofa*) in a Mediterranean coastal area. *Journal of Zoology*, 242: 411–423.
Massei, G., Roy, S. & Bunting, R., 2011. Too many hogs? A review of methods to mitigate impact by wild boar and feral hogs. *Human–Wildlife Interactions,* 5: 79–99.
Massolo, A. & Mazzoni della Stella, R., 2006. Population structure variations of wild boar *Sus scrofa* in central Italy. Italian Journal of Zoology 73: 137–144.
Melis, C., Szafrańska, P. A., Jędrzejewska, B. & Bartoń, K., 2006. Biogeographical variation in the population density of wild boar (*Sus scrofa*) in western Eurasia. *Journal of Biogeography,* 33: 803–811. DOI: 10.1111/j.1365–2699.2006.01434.x.
Meng, X. J., Lindsay, D. S. & Sriranganathan, N., 2009. Wild boars as sources for infectious diseases in livestock and humans. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 364: 2697–2707. DOI: 10.1098/rstb.2009.0086.
Mitchell, J., Dorney, W., Mayer, R. & McIlroy, J., 2009. Migration of feral pigs (*Sus scrofa*) in rainforests of north Queensland: fact or fiction? *Wildlife Re-*

search, 36: 110–116. DOI: 10.1071/WR06066.

Mueller, T. & Fagan, W. F., 2008. Search and navigation in dynamic environments – from individual behaviors to population distributions. *Oikos,* 117: 654–664. DOI: 10.1111/j.2008.0030–1299.16291.x.

Mysterud, A., 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. *Journal of Zoology*, 247: 479–486. DOI: 10.1111/j.1469–7998.1999.tb01011.x.

Mysterud, A., Meisingset, E. L., Veiberg, V., Langvatn, R., Solberg, E. J., Loe, L. E. & Stenseth, N. C., 2007. Monitoring population size of red deer *Cervus elaphus*: an evaluation of two types of census data from Norway. *Wildlife Biology,* 13: 285–298. DOI: 10.2981/0909–6396(2007)13[285:MPSORD]2.0.CO;2.

Ortigosa, L. M., García–Ruiz, J. M. & Gil, E., 1990. Land reclamation by reforestation in the Central Pyrenees. *Mountain Research and Development,* 10: 281–288.

R Development Core Team, 2011. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing (http://www.R–project.org/). Vienna.

Ramenofsky, M. & Wingfield, J. C., 2007. Regulation of migration. *Bioscience,* 57: 135–143. DOI: 10.1641/B570208.

Risch, A., Wirthner, S., Busse, M., Page–Dumroese, D. & Schütz, M., 2010. Grubbing by wild boars (*Sus scrofa* L.) and its impact on hardwood forest soil carbon dioxide emissions in Switzerland. *Oecologia,* 164: 773–784. DOI: 10.1007/s00442–010–1665–6

Rönnegård, L., Sand, H., Andrén, H., Månsson, J. & Pehrson, Å., 2008. Evaluation of four methods used to estimate population density of moose *Alces alces*. *Wildlife Biology,* 14: 358–371. DOI: 10.2981/0909–6396(2008)14[358:EOFMUT]2.0.CO;2.

Rosell, C., Navàs, F. & Romero, S., 2012. Reproduction of wild boar in a cropland and coastal wetland area: implications for management. *Animal Biodiversity and Conservation*, 35.2: 209–217.

Rossi, S., Fromont, E., Pontier, D., Cruciere, C., Hars, J., Barrat, J., Pacholek, X. & Artois, M., 2005. Incidence and persistence of classical swine fever in free–ranging wild boar (*Sus scrofa*). *Epidemiology and Infection,* 133: 559–568. DOI: 10.1017/S0950268804003553.

Rosvold, J., Halley, D. J., Hufthammer, A. K., Minagawa, M. & Andersen, R., 2010. The rise and fall of wild boar in a northern environment: evidence from stable isotopes and subfossil finds. *Holocene,* 20: 1113–1121. DOI: 10.1177/0959683610369505

Roura–Pascual, N., Pons, P., Etienne, M. & Lambert, B., 2005. Transformation of a rural landscape in the Eastern Pyrenees between 1953 and 2000. *Mountain Research and Development,* 25: 252–261. DOI: 10.1659/0276–4741(2005)025[0252:TOARLI]2.0.CO;2.

Sáez–Royuela, C. & Tellería, J. L., 1986. The increased population of the Wild Boar (*Sus scrofa* L.) in Europe. *Mammal Review,* 16: 97–101. DOI: 10.1111/j.1365–2907.1986.tb00027.x

– 1988. Las batidas como método de censo en especies de caza mayor: Aplicación al caso del jabalí (*Sus scrofa* L.) en la provincia de Burgos (Norte de España). *Doñana. Acta vertebrata,* 15(2): 215–223.

Saïd, S., Tolon, V., Brandt, S. & Baubet, E., 2012. Sex effect on habitat selection in response to hunting disturbance: the study of wild boar. *European Journal of Wildlife Research,* 58: 107–115. DOI: 10.1007/s10344–011–0548–4.

Saunders, G. & Kay, B., 1996. Movements and Home Ranges of Feral Pigs (*Sus Scrofa*) in Kosciusko National Park, New South Wales. *Wildlife Research,* 23: 711–719. DOI: 10.1071/WR9960711.

Schley, L., Dufrêne, M., Krier, A. & Frantz, A. C., 2008. Patterns of crop damage by wild boar (*Sus scrofa*) in Luxembourg over a 10–year period. *European Journal of Wildlife Research,* 54: 589–599. DOI: 10.1007/s10344–008–0183–x.

Scillitani, L., Monaco, A. & Toso, S., 2010. Do intensive drive hunts affect wild boar (*Sus scrofa*) spatial behaviour in Italy? Some evidences and management implications. *European Journal of Wildlife Research,* 56: 307–318. DOI: 10.1007/s10344–009–0314–z.

Singer, F. J., Otto, D. K., Tipton, A. R. & Hable, C. P., 1981. Home ranges, movements, and habitat use of European wild boar in Tennessee. *The Journal of Wildlife Management,* 45: 343–353.

Tellería, J. L., 2004. *Métodos de Censos en Vertebrados Terrestres*. Dpto. Biología. Animal I (Zoología de Vertebrados). Facultad de Biología, Univ. Complutense, Madrid.

Thirgood, S., Mosser, A., Tham, S., Hopcraft, G., Mwangomo, E., Mlengeya, T., Kilewo, M., Fryxell, J., Sinclair, A. R. E. & Borner, M., 2004. Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation,* 7: 113–120. DOI: 10.1017/S1367943004001404.

Welander, J., 2000. Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape. *Journal of Zoology,* 252: 263–271. DOI: 10.1111/j.1469–7998.2000.tb00621.x.

Wirthner, S., Frey, B., Busse, M. D., Schütz, M. & Risch, A. C., 2011. Effects of wild boar (*Sus scrofa* L.) rooting on the bacterial community structure in mixed–hardwood forest soils in Switzerland. *European Journal of Soil Biology,* 47: 296–302. DOI: 10.1016/j.ejsobi.2011.07.003.

Wirthner, S., Schütz, M., Page–Dumroese, D. S., Busse, M. D., Kirchner, J. W. & Risch, A. C., 2012. Do changes in soil properties after rooting by wild boars (*Sus scrofa*) affect understory vegetation in Swiss hardwood forests? *Canadian Journal of Forest Research,* 42: 585–592. DOI: 10.1139/X2012–013.

Wood, S. N., 2006. *Generalized additive models, an introduction with R.* Chapman & Hall/CRC, Boca Raton.

Zuur, A. F., Ieno, E. N. & Smith, G. M., 2007. *Analysing ecological data.* Springer, New York.