



Wild boar *Sus scrofa* mortality by hunting and wolf *Canis lupus* predation: an example in northern Spain

Authors: Nores, Carlos, Llaneza, Luis, and Álvarez, Ángel

Source: Wildlife Biology, 14(1) : 44-51

Published By: Nordic Board for Wildlife Research

URL: [https://doi.org/10.2981/0909-6396\(2008\)14\[44:WBSSMB\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2008)14[44:WBSSMB]2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Wild boar *Sus scrofa* mortality by hunting and wolf *Canis lupus* predation: an example in northern Spain

Carlos Nores, Luis Llaneza & Miguel Ángel Álvarez

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

Over the last decades, wolf *Canis lupus* predation in northern Spain has focused on wild ungulates, even though livestock and other prey, such as other carnivores and small mammals, and garbage have been available. During 1994 and 1995, we studied the impact of wolf predation on wild boar *Sus scrofa* in four study areas in Asturias, Spain. The diet of the wolf was assessed by scat collection and analysis (N = 106, 329, 372 and 649, respectively). The mortality of wild boar was deduced from density estimates and hunting records from the Nature Reserve of Somiedo. Wild boar represented 3-31% of the biomass of food found in the wolf scats in the study areas. We estimated that 75% of wild boars eaten were piglets. The wild boar mortality rate was estimated at 38% (146 dead individuals out of 385). Wolf predation was estimated to cause 12% of the mortality of wild boar and to affect 4.5% of the wild boar population. Hunting had a higher importance as a mortality factor than wolf predation (31 and 12%, respectively). Even though, a two-year study is insufficient to come to a final conclusion, our results suggest that wolf predation may have a low impact on young wild boar and that a hunting pressure of the size we found is unlikely to control the wild boar population.

Key words: *Canis lupus*, hunting, mortality, predation, Spain, *Sus scrofa*, wild boar, wolf

Carlos Nores, Luis Llaneza* & Miguel Ángel Álvarez, INDUROT, Universidad de Oviedo, Campus de Mieres, 33600 Mieres, Spain. - e-mail addresses: cnores@uniovi.es (Carlos Nores); llaneza@ctv.es (Luis Llaneza); maalvarez@indurot.uniovi.es (Miguel Ángel Álvarez)

*Present address: ARENA, Valnalón, C/ Hornos Altos s.n., 33930 Langreo, Spain

Corresponding author: Carlos Nores

Received 1 June 2005, accepted 26 December 2006

Associate Editor: Jon E. Swenson

The wolf *Canis lupus* is a natural predator of wild ungulates (Okarma 1995). However, in disturbed habitats of southern Europe, where wild ungulates had been depleted but where other abundant food sources exist, wolf has diversified its diet to include livestock, other carnivores (mainly dogs *Canis familiaris*) and small mammals. Wolf even feeds on fruits and carrion found among garbage (Meriggi & Lovari 1996).

Wild boar *Sus scrofa* has experienced the greatest expansion (Nores et al. 1995). The increase in the number of wild boar has occurred over almost all of Europe (Sáez-Royuela & Tellería 1986). In Spain it took place around the 1960s (Tellería & Sáez-Royuela 1985), although in the Cantabrian area, and particularly in Asturias, it did not occur until the late 1980s. One of the consequences of the recent increase in wild ungulate numbers has been a

change in the feeding behaviour of wolves (Meriggi et al. 1996).

It has been suggested that the increase in wild boar is related to decreases in the wolf populations (Tellería & Sáez-Royuela 1985, Gerard et al. 1991), but this has not been adequately explored. The most important studies carried out on the subject have been conducted in the Białowieża Primeval Forest in Poland (Okarma et al. 1995, Jędrzejewski et al. 2000, 2002), in an environment that differs very much from the environment in southern Europe. Melis et al. (2006) found that the presence of wolves has a limited effect on boar population density in Europe as a whole, albeit they were not able to elucidate whether the impact of wolf predation on wild boar actually declines northwards or whether the harsh winters have a greater bearing on determining wild boar densities at high latitudes, and whether predator-inflicted mortality is compensatory or not. In this article, we aim to describe the importance of wild boar as a wolf prey in the Cantabrian Mountain Range, northern Spain. We also compare the effect of wolf predation and hunting on wild boar mortality in the Somiedo Natural Park to test how, if at all, wolf predation could control wild boar populations in southern Europe.

Study area and methods

Asturias is a region located between the north coast of Spain and the Cantabrian Mountain Range (Fig 1). It has an oceanic climate with altitudes ranging within 0-2,648 m a.s.l. and it covers 10,500 km², in most of which wolf and wild boar are present.

The Nature Reserve of Somiedo covers almost 300 km² on the Asturian side of the western Cantabrian Mountain Range, with altitudes ranging within 800-2,100 m a.s.l. The most abundant type of habitat is heath (41%), followed by deciduous forests (23%) and pastures (18%), and some rocky outcrops, subalpine

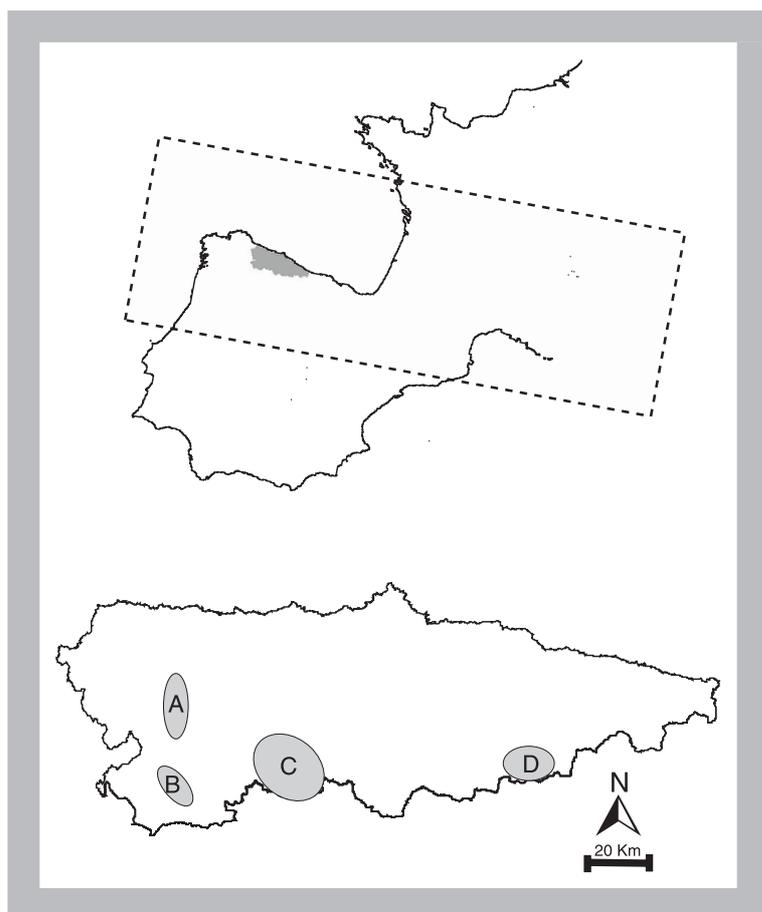


Figure 1. Overall location of the study area in Asturias, northern Spain, with indication of the study areas A-D from which the wolf scats were collected. The Nature Reserve of Somiedo is area C.

vegetation, evergreen forests, shrubs and urban settlements. It is a well-conserved mountain pasture land, with a human density of 6.2 inhabitants/km², and abundant livestock kept in an extensive free-grazing system. The fauna includes large mammals such as brown bear *Ursus arctos*, wolf, red deer *Cervus elaphus*, southern chamois *Rupicapra pyrenaica*, roe deer *Capreolus capreolus* and wild boar, of which wild boar has been hunted in hunting drives since 1966.

We studied the diet of wolves in four different areas of Asturias, each covering 50-100 km² (see Fig. 1), by collecting scats during March 1994-March 1995. We based prey identification on hair, hooves and bones, and we used several identification keys (e.g. Faliú et al. 1980, Teerink 1991) as well as a local hair collection. In some cases, the age class of the prey items could be defined through the presence of smaller sized remains such as hooves and small bones in the scats. We expressed the diet in terms of percentage of biomass ingested using the equation of Floyd et al. (1978), revised by Weaver (1993), and followed the recommendations of Ciucci et al. (1996); (Table 1). The biomass of Asturian animals was from Llana et al. (1996).

We carried out two wild boar population estimates in the Natural Reserve of Somiedo in 1994 and 1995 using the procedure described by Nores et al. (2000). The process is an adaptation of the method used by Langvatn (1977) to estimate deer during rutting (roaring stag estimation), which considers the social structure of the groups observed. The method has often been used in mountainous areas with a low detectability (Albaret et al. 1986, Bobek et al. 1986, Mazzarone et al. 1991) and it is an

adaptation of the estimation method named Index and Control method (Caughley 1977). In our case, we used the minimum number of family groups obtained by all procedures available (random walks to locate piglet footprints, automatic cameras and telescopic watching sites) as the control; the estimation was made using the proportion between the number of family groups observed and any other type of wild boar group (single or grouped subadult or adult individuals) as indices.

In the study areas, we used the number of wild boar killed by hunters per day (catch-per-unit-effort) during the hunting season as a relative density index. We calculated mortality by taking into consideration that the number of individuals that were >1 year old in 1995 were the survivors of the total estimated population in 1994, following the procedure outlined by Johnson (1994) for the estimation of the mortality ratios of population sizes.

We estimated the number of wild boar killed by wolves in the Nature Reserve of Somiedo in two different ways. First, we compared the proportion of wild boar and domestic species in the wolf diet (scats) with the number of domestic animals killed by wolves with the claims for damages filed by the Park. We thus estimated the number of wild boar killed by wolves on the basis of the percentage of wild boar, sheep *Ovis aries* and domestic goat *Capra aegagrus hircus* biomass present in the wolf diet (corrected by the mean weight of every species), and we compared their values with the sheep and domestic goats killed by wolves in Somiedo during the same period. We did not use the proportion of horse *Equus caballus* and cattle because, due to their larger size, the carcasses are usually removed by the owners before wolves can eat them up completely and so would be less represented in the scats.

Secondly, we used an alternative method based on Fuller (1989), assessing that a 20-kg wolf would eat 438 kg of food per year. By multiplying this sum by the intake of biomass percentage (11.9% of biomass consumed ~52.12 kg wild boar) and dividing it by the average weight of an ingested wild boar (three piglets per adult averaging 33 kg per adult individual), a wolf can be estimated to consume 1.6 wild boars annually.

We used the Spearman coefficient of rank correlation (r_s) as a non-parametric correlation coefficient to test the relation between wild ungulate abundance in the wolf diet and their abundance as a prey, because our data did not show a normal

Table 1. Percentage of prey biomass in wolf scats collected in the areas A-D (see Fig. 1) in Asturias, northern Spain, during March 1994-March 1995. N gives the number of scats collected.

Prey species	Area A (N = 649)	Area B (N = 372)	Area C (N = 329)	Area D (N = 106)
Wild boar	6.0	31.0	11.9	2.8
Roe deer	5.5	42.4		
Roe deer & red deer			41.3	43.8
Chamois		2.8	5.8	24.3
Sheep	2.3	0.5	4.9	6.5
Goat	9.5	5.1	10.4	4.7
Cattle	4.0		4.0	1.9
Horse	61.5	7.4	4.6	1.9
Small carnivores	2.0	2.8	1.22	
Small mammals			2.1	
Others	9.2	8.1	13.5	14.1

bivariate distribution. We used only four ranks (just within the limit for using rank correlation tests). Due to the small amount of data available, we ascribed greater importance to the P-value as a means of comparing the correlation abundance-consumption of the different species in relative terms than the correlation coefficient obtained itself. We used the Fisher's exact test to compare selective wolf predation on piglets with numbers in relation to non-piglets in the scats as well as in living animals sampled in the field. All estimates are given \pm SE.

Results

Wild boar in wolf diet and as a game species

The percentage of wild boar biomass in the diet of wolves in Asturias ranged within 2.8-31% among study areas (A-D in Fig. 1), and ranked from second to fourth among prey, depending on the area. It was ranked after roe deer or after horse, sheep and goat, red deer or chamois (see Table 1).

The percentage of wild boar biomass in the wolf prey diet was unrelated to the relative density of wild boar ($r_s = -0.2$, $N = 4$, $P = 0.8$). Contrasting this, other wild prey such as deer (roe + red deer; $r_s = 0.667$, $N = 4$; $P = 0.174$) and chamois ($r_s = 1$, $N = 3$; $P = 0$) exhibited more obvious relations between abundance and consumption. Nevertheless, wild boar consumption did reveal a certain negative correlation with the Simpson's dominance index of the remaining ungulate species ($r_s = -0.8$; $N = 4$, $P = 0.2$; Table 2).

Table 2. Density of some wolf prey species in the areas A-D in Asturias, northern Spain, during the 1994/95 hunting season. Data on wild boar and deer are presented as relative density (number of individuals killed by hunters per day) and on other prey species as absolute densities (individuals per km²). NP indicates that the species was not present in the area. D gives the Simpson's Dominance Index of wolf prey, without including wild boar. Data on chamois were obtained from transect counts, and on sheep, goat, cattle and horse from official veterinary records.

Prey species	Area A	Area B	Area C	Area D
Wild boar	0.53	0.82	0.75	1.43
Red deer	NP	NP	0.80	0.74
Roe deer	0.38	0.83	0.54	0.85
Chamois	NP	0.76	6.40	18.89
Sheep	1.4	2.4	4.2	1.4
Goats	9.5	5.1	10.4	4.7
Cattle	10.3	18.4	20.1	15.1
Horse	10.0	0.1	0.9	1.0
D	0.401	0.196	0.210	0.278

Table 3. Seasonal variation of wild boar biomass (in %) in wolf diet in the areas A-D in Asturias, northern Spain. The highest values of wild boar consumption are italicised. N gives the number of scats collected.

	Area A (N = 649)	Area B (N = 372)	Area C (N = 329)	Area D (N = 106)
Spring	0	26.0	8.3	1.7
Summer	4.6	28.6	7.4	4.8
Autumn	9.9	28.9	11.4	0
Winter	9.5	<i>42.0</i>	<i>19.4</i>	<i>5.9</i>
No. of wild boar items	36.0	122.0	39.0	3.0
% of wild boar biomass	6.0	30.9	11.9	2.8

Wild boar consumption was generally greater during winter than during spring, summer and autumn (Table 3). In spring and summer, wolf predation was focused on juveniles rather than on adults. Of the wild boar in wolf scats whose age could be determined ($N = 16$), 75% were in their first year of life, compared with an estimated 21% of piglets in the population in summer (Nores et al. 2000). This difference was highly significant (Fisher's exact test: $P = 0.0036$, $N = 62$).

Wild boar mortality in the Natural Park of Somiedo

Wild boar density and demography in the Nature Reserve of Somiedo were estimated during 1994 and 1995 (Nores et al. 2000). The population loss rate (mortality + emigration) can be estimated by comparing the data from both years. Although we had no data on immigration and emigration rates, we assumed that they were balanced as wild boar numbers hunted per day remained stable for the whole of the Regional Game Reserves from 1990 to 1995 (Teresa Sánchez Corominas, pers. comm.).

Following the procedure outlined by Johnson (1994), of the total of 385 ± 63 (80 piglets and 305 non-juveniles) estimated wild boar in the Nature Reserve of Somiedo in 1994, 239 were ≥ 1 -year-olds in 1995 (350 ± 60 animals estimated of which 111 were piglets). This leads to an annual survival rate of 0.621. Of the estimated 146 individuals (38%) that died, 45% were killed during the hunting season, i.e. an estimated harvest of 11.7%.

Based on 10 sheep and nine domestic goats killed by wolves in 1994, we estimated that 16.2 ± 5.4 wild boars were killed by wolves. These kills represented 4.2% of the 1994 wild boar population (11.1% of dead wild boar). Using the Fuller (1989) method, and assuming seven wolves in each of the two known reproductive packs in Somiedo, which used 200 km²

(see Vilà et al. 1990), we estimated that an average of about 11 wolves used the 300 km² of the whole Nature Reserve. We estimated that at least 17.5 wild boars were to be killed by wolves (4.5% of the population and 12% of the estimated numbers of dead wild boar). The two methods gave similar results.

Discussion

About the methodology

Our methods give approximations of mortality causes. A more precise method should be used to test our conclusions, using mark-recapture and long-term radio-tracking methods. Among possible biases are: the estimation of the mortality rate depends on population estimates, and counting wild boar is well-known to be a difficult task, because of their wide-ranging movements, their preference for dense forests and their highly aggregated distribution patterns (Barret 1982). But while the numbers of wild boars shot or killed by wolves are independent of the wild boar population estimates, they are not independent of the other causes of death that influence the wild boar population.

Fuller's (1989) method for calculating the number of wild boar consumed by wolves is based on a fixed intake of meat by each wolf. The intake estimates made in Central Europe (i.e. Poland; Jędrzejewski et al. 2002) are higher, but daily intake increases with snow cover, which enhances predation efficiency by increasing prey vulnerability and the coherence of the wolf packs. The smaller amounts of snow in Somiedo and the coincidence of the estimates obtained in each of the methods appear to reveal that our estimation of the amount of wild boar consumed by wolves may in fact be quite realistic.

Nevertheless, wolf predation might be smaller than recorded in our estimation, because we were unable to determine whether wild boar in wolf scats came from an actual predation or were consumed as carrion. Only four of the 45 shot wild boars were wounded and did not recover, but illegal hunting (wild boars are illicitly snared in Somiedo to avoid damages to meadows) and natural mortality other than predation must be included as 'other causes'.

It is also difficult to generalise our results on the mortality of wild boar in the Somiedo National Park because they were obtained over just a year. The acorn crop in the autumn of 1994 was slightly below the mean (the mast was in the 42 percentile;

Domínguez 1996). Yet, 1994/95 was a very mild winter; i.e. >85% of all the recorded December months were colder. So, the mortality during 1994/95 may have been lower than usually.

Wild boar as wolf prey

The diet of the wolf in Asturias is very variable even in locations which are not far apart. The distances from area A to B and from area B to C are < 25 km and the differences in consumption of wild boar are quite large (five times higher in area B than in A and nearly three times higher in B than in C). Similar variations are seen in other prey species, particularly in deer (very scarce in area A), horse (the main prey in area A) and chamois (very abundant in area D). Cattle, although abundant in all the areas, are seldom preyed due to, among other reasons, the greater attention being paid by farmers and to the fact that the animals are stabled for half of the year. The frequency of wild boar occurrence in the wolf diet does not seem to depend on the density of the species, because the consumption of wild boar appears to be inversely related to the availability of other prey, as revealed by the negative correlation with the dominance of the rest of the ungulate community. A possible explanation for wolf consumption of wild boar in our study area might be ascribed to the differences in the availability or accessibility of alternative prey species.

Consumption of young wild boar by wolves, as witnessed in Somiedo, is a well-known phenomenon. In the Białowieża Forest (Poland), young wild boar represent as much as 94% of the wild boar eaten by wolves (Jędrzejewski et al. 1992), and in the northern Apennines (Italy) they represent >77% of occurrences (Mattioli et al. 1995). This may be ascribed to a higher vulnerability of dispersing juveniles to predation than of adults (Mattioli et al. 1995, Meriggi & Lovari 1996).

In Białowieża Forest, the importance of wolf predation in ungulate mortality varies considerably among years and depending on winter severity and prey availability, but deaths caused by diseases and starvation seem to be more important than killings resulting from wolf predation (Okarma 1995). Wild boar winter deaths were mainly influenced by snow cover and the acorn crop in the previous year (Okarma et al. 1995).

The influence of wolf predation on wild boar populations may vary from one site to another. Kanzaki et al. (1998) believe that in Bieszczady Mountains (Poland), with low densities of wild boar and high

densities of wolf, predation may be more decisive than other environmental factors (e.g. winter temperature, snow cover and beech nut crop) on wild boar population dynamics. However, there are two factors that should be kept in mind in order to interpret these results: 1) Although the density of wolves in these Polish mountains was similar to the density in Somiedo, the density of the wild boar in the Bieszczady Mountains was less than half of the density in Somiedo; 2) Kanzaki et al. (1998) did not consider the time lags in the correlation between wild boar density and the other environmental factors, yet these are fundamental in other studies (Neet 1995). In contrast, other studies of wolf predation reveal that it has a low impact on wild boar populations. At least, that is the case in the Białowieża Forest (Jędrzejewska & Jędrzejewski 1998, 2005 in Melis et al. 2006), where the wolf density is similar to the density in Somiedo and the wild boar density is higher. The predation pattern in the Białowieża Forest is similar to the pattern in Somiedo, both in terms of the selection of piglets and young individuals, as well as in terms of the percentage of the population killed (4-8%; Jędrzejewski et al. 2000, 2002).

Wild boar as big game

In Asturias, wild boar is a secondary prey species for the wolf, and also the most widely hunted big game. During the 1994/95 season, 1,744 wild boars were legally killed in Asturias, which is twice as many as of all the other big game species combined (i.e. red deer, roe deer, southern chamois and fallow deer). In the 2005/06 season, the number of wild boar killed increased to 6,284 (Teresa Sánchez-Corominas, pers. comm.). The catch-per-unit-effort annual increase of wild boar in Somiedo is >7% (Uzal & Nores 2004), slightly less than for the whole of Asturias.

According to our study, the annual mortality of wild boar as estimated by use of our two methods is comparable to the mortality rate recorded in areas of low hunting pressure, such as Petit Pierre (Gaillard et al. 1987) or Camarge (Spitz 1989). The wild boar harvest in the Nature Reserve of Somiedo, and in general in Asturias, is low and smaller than harvests obtained in other regions in northern Spain, which varies from 17 to 37% of the population estimated by drive counts (Sáez-Royuela & Tellería 1988, Lerános & Castián 1996, Herrero 2003). It clearly remains below the harvest levels that have been reported in many areas of Europe and which

usually exceed 30% (Spitz et al. 1984, Gaillard et al. 1987, Boitani et al. 1995). The scarcely harvested populations in northern Spain are characterised by higher juvenile mortality and higher survival of individuals >3 years old (Nores et al. 2000), as reported for other wild boar populations with low hunting pressure (Jeziński 1977, Gaillard et al. 1987).

In Somiedo, hunting and wolf predation, even if both were similar in their intensity, might have different demographic importance, as they operate on different age groups. Because the wolf exerts a higher pressure on juveniles rather than on adults during winter in Somiedo, it allows a relative greater survival of the reproductive animals, thus permitting them to compensate for the losses more easily in the year to come. On the contrary, the mortality caused by hunting drives tends to affect the adult age groups more (Milkowski & Wojcik 1984), and a higher proportion of reproductive females are killed. Nonetheless, the importance of the age groups that have the greatest bearing on population increase varies depending on the availability of food; during mast years the survival of juveniles that become breeders is more important, whereas during years of scant yield (small or no crops), in the absence of juvenile reproduction, the most important segment from the population dynamics perspective is the adult females (Bieber & Ruf 2005). So, wolf predation could acquire a more important role in years of abundant resources for wild boar, but their control is not such as to avoid wild boar increase.

On a European scale, Melis et al. (2006) stated that predation by wolves appears to have a weaker effect on wild boar density than winter temperatures and vegetation productivity, but they were unable to quantify the role of hunting. Even so, most studies have concluded that it is very unlikely that sport hunting can control wild boar density (Boitani et al. 1995, Csányi 1995), although high hunting pressures may change the population structure (Gaillard et al. 1987). In our study, wolf predation seemed to have less importance as a control means of population dynamics than did hunting.

Acknowledgements - the basis for this paper was a review of the results from two different projects included in the SV-PA-94-003 grant sponsored by the Principado de Asturias in 1994 and 1995. We are especially grateful to Teresa Sánchez Corominas for supplying unpublished data from the files in the Administration of the Principado de Asturias and from unpublished reports; to Norberto Corral, Gil González Rodríguez and Ana Colubi from the Department of Statistics of the

University of Oviedo; to Pedro García-Rovés, Sara García Inclán (INDUROT), Juan Carlos Blanco and Jon E. Swenson for their help, and to Yolanda Harts-horne and Priscilla Chase for revising the language.

References

- Albaret, M., Lartiges, A. & Peroux, R. 1986: Recensement des cerfs au brame. Essais réalisées sur la Pinatell d'Allanche (Cantal). - *Bulletin Mensuel de l'Office National de la Chasse* 132: 21-26. (In French).
- Barret, R.H. 1982: Wild pigs. - In: Davies, D.E. (Ed.): *Handbook of census methods for terrestrial vertebrates*. - CRC Press, Boca Raton, pp. 243-244.
- Bieber, C. & Ruf, T. 2005: Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. - *Journal of Applied Ecology* 42: 1203-1213.
- Bobek, B., Perzanowski, K. & Zielinski, J. 1986: Red deer population census in mountains: testing of an alternative method. - *Acta Theriologica* 31: 423-431.
- Boitani, L., Trapanese, P., Mattei, L. & Nonis, D. 1995: Demography of a wild boar (*Sus scrofa*, L.) population in Tuscany, Italy. - *Gibier Faune Sauvage* 12: 109-132.
- Csányi, S. 1995: Wild boar population dynamics and management in Hungary. - *Ibex Journal of Mountain Ecology* 3: 222-225.
- Caughley, G. 1977: Analysis of vertebrate populations. - John Wiley & Sons, Chichester, 234 pp.
- Ciucci, P., Boitani, L., Pelliccioni, E.R., Rocco, M. & Gui, I. 1996: A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. - *Wildlife Biology* 2(1): 37-48.
- Domínguez, J.A. 1996: Producción anual de semillas y hojarasca en robledales y hayedos de la Reserva Biológica de Muniellos. - M.Sc. thesis, Universidad de Oviedo, Oviedo, 18 pp. (In Spanish).
- Faliú, L., Lignareux, Y. & Barrat, J. 1980: Identificación des poils de mammifères pyrénéens. - *Doñana, Acta Vertebrata* 7: 125-212. (In French).
- Floyd, T.J., Mech, L.D. & Jordan, P.A. 1978: Relating wolf scat contents to prey consumed. - *Journal of Wildlife Management* 42(3): 528-532.
- Fuller, T.K. 1989: Population dynamics of wolves in north central Minnesota. - *Wildlife Monographs* 105: 1-41.
- Gaillard, J-M., Vassant, J. & Klein, F. 1987: Quelques caractéristiques de la dynamique des populations de sangliers (*Sus scrofa scrofa*) en milieu chassé. (In French with an English summary: Some characteristics of the population dynamics of wild boar (*Sus scrofa scrofa*) in a hunted environment) - *Gibier Faune Sauvage* 4: 31-47.
- Gerard, J.F., Teillaud, P., Spitz, F., Maugeat, R. & Campan, R. 1991: Le sanglier. - *Revue d'Ecologie (Terre Vie), Supplément* 6: 11-66. (In French).
- Herrero, J. 2003: Adaptación funcional del jabalí (*Sus scrofa* L.) a un ecosistema forestal y a un sistema agrario intensivo en Aragón. - Consejo de Protección de la Naturaleza de Aragón, Zaragoza: 159 pp. (In Spanish).
- Jędrzejewska, B. & Jędrzejewski, W. 1998: Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. - *Ecological Studies* 135. Springer-Verlag, Berlin, 500 pp.
- Jędrzejewski, W., Jędrzejewska, B., Okarma, H. & Ruprecht, A.L. 1992: Wolf predation and snow cover as mortality factors in the ungulate community of the Białowieża National Park, Poland. - *Oecologia* 90(1): 27-36.
- Jędrzejewski, W., Jędrzejewska, B., Okarma, H., Schmidt, K., Zub, K. & Musiani, M. 2000: Prey selection and predation by wolves in Białowieża Primeval Forest, Poland. - *Journal of Mammalogy* 81(1): 197-212.
- Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., Selva, N., Zub, K. & Szymura, L. 2002: Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). - *Ecology* 83(5): 1341-1356.
- Jeziński, W. 1977: Longevity and mortality rate in a population of wild boar. - *Acta Theriologica* 32: 337-348.
- Johnson, D.H. 1994: Population analysis. - In: Bookhout, T.A. (Ed.): *Research and management techniques for wildlife and habitats*. The Wildlife Society, Bethesda, pp. 419-444.
- Kanzaki, N., Perzanowski, K. & Nowosad, M. 1998: Factors affecting wild boar (*Sus scrofa*) population dynamics in Bieszczady, Poland. - *Gibier Faune Sauvage* 15 (Hors série Tome 3): 1171-1178.
- Langvatn, R. 1977: Social behaviour and population structure as a basis for censusing red deer populations. - In: Peterle, T.J. (Ed.): *XIII International Congress of Game Biologists*. The Wildlife Society, Wildlife Management Institute, Washington D.C., pp. 77-89.
- Leránz, I. & Castián, E. 1996: Evolución de la población del jabalí (*Sus scrofa* L., 1758) en Navarra (N Península Ibérica). (In Spanish with an English summary: Evolution of wild boar (*Sus scrofa*, L., 1758) population in Navarra (N Iberian Peninsula). - *Miscellanea Zoologica* 19: 133-139.
- Llaneza, L., Fernández, A. & Nores, C. 1996: Dieta del lobo en dos zonas de Asturias (España) que difieren en carga ganadera. (In Spanish with an English summary: The diet of the wolf in two areas from Asturias (Spain) with different livestock occurrence). - *Doñana, Acta Vertebrata* 23: 201-213.
- Mattioli, L., Apollonio, M., Lovari, C., Siemone, N. & Crudele, G. 1995: Wild boar as the main prey of wolf in an area of Northern Apennines (Italy). - *Ibex, Journal of Mountain Ecology* 3: 212.
- Mazzarone, V., Siemone, N., Pedone, P., Lovari, C. & Mattioli, L. 1991: A method of red deer (*Cervus elaphus* L.) census during the roaring period in a forested

- area of the Northern Apennines (Central Italy). - In: Csányi, S. & Ernhaft, J. (Eds.); XX Congress International Union of Game Biologists, Transaction Part 1. University of Agricultural Sciences, Gödöllő, Hungary, pp. 140-145.
- Melis, C., Szafrńska, 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.
- Meriggi, A., Grangi, A., Mateucci, C. & Sacci, O. 1996: The feeding habits of wolves in relation to large prey availability in Northern Italy. - *Ecography* 19: 287-295.
- Meriggi, A. & Lovari, S. 1996: A review of wolf predation in Southern Europe: does the wolf prefer wild prey to livestock? - *Journal of Applied Ecology* 33: 1561-1571.
- Milkowski, L. & Wojcik, J.M. 1984: Structure of wild boar harvest in the Białowieża Primeval Forest. - *Acta Theriologica* 29: 337-347.
- Neet, C.R. 1995: Population dynamics and management of *Sus scrofa* in western Switzerland: A statistical modelling approach. - *Ibex, Journal of Mountain Ecology* 3: 188-191.
- Nores, C., Fernández, A. & Corral, N. 2000: Estimación de la población de jabalí (*Sus scrofa*) por recuento de grupos familiares. (In Spanish with an English summary: Estimating wild boar (*Sus scrofa*) population by counting family herds). - *Naturalia Cantabrigiae* 1: 53-59.
- Nores, C., González, F. & García, P. 1995: Wild boar distribution trends in the last two centuries: an example in Northern Spain. - *Ibex, Journal of Mountain Ecology* 3: 137-140.
- Okarma, H. 1995: The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. - *Acta Theriologica* 40: 335-386.
- Okarma, H., Jędrzejewska, B., Jędrzejewski, W., Krański, Z. & Milkowski, L. 1995: The roles of predation, snow cover, acorn crop, and man-related factors on ungulate mortality in Białowieża Primeval Forest, Poland. - *Acta Theriologica* 40: 197-217.
- Sáez-Royuela, C. & Tellería, J.L. 1986: The increased population of the wild boar (*Sus scrofa* L.) in Europe. - *Mammal Review* 16: 97-101.
- Sáez-Royuela, C. & Tellería, J.L. 1988: Las batidas como método de censo de especies de caza mayor: el caso del jabalí (*Sus scrofa*) en la provincia de Burgos (Norte de España). (In Spanish with an English summary: The use of battues in the big game study). - *Doñana, Acta Vertebrata* 15: 215-223.
- Spitz, F. 1989: Mortalité et dispersion chez le sanglier (*Sus scrofa*) de Camargue. (In French with an English summary: Wild boar (*Sus scrofa*) mortality and dispersion in the Camargue). - *Gibier Faune Sauvage* 6: 27-42.
- Spitz, F., Janeau, J. & Valet, G. 1984: Éléments de démographie du sanglier (*Sus scrofa*) dans la Grésigne. - *Acta Oecologica (Oecologia Applicata)*, 5: 43-59. (In French with an English summary).
- Teerink, B.J. 1991: Atlas and identification key hair of West-European mammals. - Cambridge University Press, Cambridge, 224 pp.
- Tellería, J.L. & Sáez-Royuela, C. 1985: L'évolution démographique du sanglier (*Sus scrofa*) en Espagne. - *Mammalia* 49: 195-202. (In French with an English summary).
- Uzal, A. & Nores, C. 2004: Endogenous and exogenous constraints in the population changes of wild boar (*Sus scrofa* Linnaeus, 1758). - *Galemys* 16: 83-98.
- Vilà, C., Urios, V. & Castroviejo, J. 1990: Ecología del lobo en La Cabrera (León) y La Carballeda (Zamora). - In: Blanco, J.C., Cuesta, L. & Reig, S. (Eds.); *El lobo (Canis lupus) en España. Situación, problemática y apuntes sobre su ecología*. - ICONA, Madrid, pp. 95-108. (In Spanish).
- Weaver, J.L. 1993: Refining the equation for interpreting prey occurrence in gray wolf scats. - *Journal of Wildlife Management* 57: 534-538.