Historical dynamics of a declining wolf population: persecution vs. prey reduction

José María Fernández, Nerea Ruiz de Azua

Eur J Wildl Res (2010) 56:169–179
DOI 10.1007/s10344-009-0300-5

ORIGINAL PAPER

Historical dynamics of a declining wolf population: persecution vs. prey reduction

José María Fernández · Nerea Ruiz de Azua

Received: 21 January 2009 / Revised: 10 May 2009 / Accepted: 23 June 2009 / Published online: 14 July 2009

Abstract Using records from archives detailing bounties for wolves killed in northern Spain during the eighteenth and nineteenth centuries, we investigated demographic and spatial distribution parameters of the population to determine whether direct persecution or prey availability was responsible for the observed population decline. Captures of adult, subadult, and young individuals, including those of litters, showed a downward trend. Progressive decreases in age ratio and litter size, and the increase in the proportion of males, were compatible with a population under food stress, driven by the extinction of wild ungulates, the sharp reduction in livestock numbers, and the lack of alternative prey. The immigration and dispersal process does not seem to have functioned under such conditions. In the study area, where strychnine was not used until the end of the nineteenth century, the broadly accepted idea of human persecution having an exclusive or primary role in wolf decline does not necessarily apply.

Keywords *Canis lupus* · Wolf · Persecution · Prey · Spain · Mortality

Introduction

Understanding the role of interacting factors leading to population decline and extinction is currently a central topic in conservation biology (Green 2002; Mills 2007; Carrete et al. 2007). In particular, the conservation of carnivore populations needs to be based on a complete knowledge of specific causes of decline, so as to permit implementation of efficient adaptive strategies (Woodroffe 2001). Scientific literature has generally attributed the long-term decline in most gray wolf (*Canis lupus*) populations to the direct effect of persecution, ascribing a minor or secondary role to prey reduction (Mech 1995; Woodroffe 2001; Fuller et al. 2003; Nilsson 2003). But recently, some emphasis has been put on assessing which of these two is the prevalent factor and on identifying the response to variations in each (Johnson 2004). In North America, it has been proposed that the lack of wild ungulates could have driven predation on livestock, therefore, promoting control and extirpation (Phillips et al. 2004). In Europe, it has been widely accepted that the main regulating factor for wolf populations has been the level of compatibility with human activities, but the ultimate reasons for decline have rarely been assessed (Andersen et al. 2006).

The resilience of this species in non-isolated populations, even under intense persecution, relates to its ability to disperse from refugia (immigration) and to increase in reproductive output (proportion of breeding females, litter size, and pup survival), which in turn depends on available per capita trophic resources (Mech 1981; Linnell et al. 2005). In this context, prey abundance and its accessibility could be a factor related to decline, once the behavioral and diet flexibility of the species has been taken into account (Mech and Peterson 2003; Espuno 2004). Thus, if prey reduction is responsible for a decline in a given wolf population, coherent demographic and reproductive responses should be expected.

To test this hypothesis, demographic data suitable for analysis as long-term time series are needed (Johnson 2004), but this is rarely available in current populations. The analyses of declines in historic and regional contexts

Communicated by: H. Kierdorf

J. M. Fernández (✉) · N. Ruiz de Azua
Instituto Alavés de la Naturaleza,
Calle de Pedro de Asúa, 2,
01008 Vitoria, Álava, Spain
e-mail: elcorralin@yahoo.es

may prove to be helpful (Fuller et al. 2003; Boitani et al. 2004) because such data can be extracted from records of official bounties paid for wolf kills, a surrogate for wolf occurrence and abundance (Beaufort 1987; Orsini 1996; Elgmork 1996; Grau et al. 1990; Rico and Torrente 2000; Riley et al. 2004). These bounties were a common mechanism in Europe and North America in the seventeenth, eighteenth, and nineteenth centuries, in an attempt to stimulate eradication and solve the long-lasting conflict with pests and dangerous animals (Sillero-Zubiri and Schwitzer 2004).

Western European wolf populations suffered from a steep spatial and numerical decline throughout the seventeenth and eighteenth centuries, leading to their extinction in several countries (Yalden 1999; Boitani 2003; Mech and Boitani 2004). Iberian populations persisted longer (Blanco et al. 1992; Boitani 2003), and their decline, along with regional extinctions, took place largely in the nineteenth century (Caussimont 1981; Grande del Brío 1984; Valverde and Teruelo 2001). This process was described in terms of range reduction using encyclopedic or geographic literature over the last few centuries, containing occurrence data about wolves in a number of locations.

The availability of hunting records with explicit time and space references allows the development of datasets which can be analyzed from an ecological perspective and helps to test predicted demographic responses. In this way, our goals are: (1) to explore the use of this type of information to provide knowledge about the numbers and reproductive output of a wolf population in decline, (2) to test whether observed response supports either the “persecution” or “prey reduction” hypothesis, and (3) to describe the spatial distribution of such a population.

Materials and methods

Study area

The Basque country is a region of 7,230 km^2 situated in northern Spain, straddling the Atlantic and Mediterranean biogeographic regions and made up of three administrative provinces. Widely scattered human settlements, greater population density, and private land ownership in the northern half of the area contrast with the social and environmental situation in the southern half, where public forest ownership was maintained and sustainable exploitation of woods persisted (Aragón 2003). The early consequences of these processes were forest depletion through deforestation in the northern half (Garayo 1992).

At a landscape scale, this territory plays an important role as a connecting area for large mammal populations between the main Spanish mountain chains, the Pyrenees and the Cantabrian range. The east–west alignment of Basque mountains strengthens this biological corridor. There is theoretical and empirical evidence of this function, including the immigration dynamics of roe deer (*Capreolus capreolus*) and wolves in the last decades of the twentieth century (Sáenz de Buruaga et al. 2000; Echegaray et al. 2007). Roe deer along with livestock constitute the staple food of wolves in northern Spain, judging from current data (Cuesta et al. 1991).

Data

In northern Spain, institutional action against wolves was implemented through bounties as a means of improving conditions for extensive livestock rearing. Bounties were managed by local authorities and generated an economic and bureaucratic activity that can be traced today. The search for and gathering of reports related to bounties were carried out in the historical archives of provincial councils and again, separately, in municipal councils. Four types of sufficiently explicit reports were found: applications from hunters, certificates issued by local authorities, receipts issued by treasurers, and annual account book entries.

In the provincial archives, data on locality, site, number of individuals, age (“adult and young” or “pup”), sex, hunting method, and date of kill were usually recorded. These references to spatial, temporal, and biological features were due to two main reasons: the existence of bounty rates according to so-called individual reproductive value (around 500, 400, and 100 Spanish *reales* each for adult female, adult male, and pup, respectively) and to avoid fraud. The time span studied in provincial archives was from 1805 until 1905. Records corresponding to the eighteenth and twentieth centuries were few and far between: in the first case through loss of files and in the second as a result of the virtual extinction of the wolf population.

As far as the archives of municipal councils are concerned, account books mentioning bounties paid annually for wolves and red foxes (*Vulpes vulpes*) bagged were found for the periods 1693–1804 and 1813–1841. Data about location, date of kill, sex, and age were mostly absent in these files, with just the number of individuals and the amount of money issued being reported.

Analysis

Provincial and municipal datasets were analyzed separately. The information compiled was stored in a Microsoft Access database. The information about localities where the wolves were captured was transformed into municipalities—in agreement with modern boundaries, which by and large have not changed with respect to those of the nineteenth century—since this was the unequivocal territorial unit.

Specific dates were subsumed into months. The distribution of the available data made it necessary to group these in 10-year periods and to consider the most appropriate intervals in each situation. To perform a spatial analysis, a geographical information system (Arcview 3.2 program, spatial analyst module and assign proximity function) was used. Statistical analyses were performed with the programs SPSS and Statistica, using association and correlation tests, linear regression, analysis of variance (ANOVA), and time series analysis (single spectrum Fourier). Spectrum analysis explores cyclic long-term patterns of data, decomposing a complex time series with cyclical frequency components into a few underlying sinusoidal (sine and cosine) functions, estimating the relative importance of each. Peak values in a periodogram are interpreted as the period of oscillation for the observed variable (Chatfield 2003).

Results

Trend in young and adult records

We compiled 293 records of adult and young wolves (including subadults), with an age in excess of 3–4 months, captured during 1805–1905 and corresponding to a total of 308 individuals (X_{year}=3.05 wolves, s=5.73, max=32, min=0). Most of the records (96%) referred to just one wolf killed. With regard to the first half of the century, the series of records was interrupted for three periods (1806–1813, 1817–1821, and 1835–1837). The box plot in Fig. 1 illustrates the difference regarding hunting bags between 1814 and 1853, with extended annual variation and high upper limits, and 1854–1893, with narrow ranges and upper limits close to zero. The most extreme records (1805 to 1813 and 1894 to 1905) were excluded.

Young and adult hunting methods

The hunting method was assessed for 165 wolves. About 54.5% were captured by means of leg-hold traps and 15.1% by means of collective actions (drive hunts). To the latter percentage must be added another 16.9% of drive hunts associated with the use of *loberas* (traditional Spanish and Portuguese constructions with long convergent walls ending in a pit, existing only at the western end of the study area). In 12.1% of the cases, death by shooting was mentioned, and only in 1.2% death by poison.

By displaying proportions of every cause of mortality for 10-year periods (Fig. 2), a downward trend was observed in the use of leg-hold traps (linear regression with arcsine transformation and analysis of significance with one-way ANOVA; b=−0.184, F=17.705, p=0.052) and an upward trend in that of drive hunts (b=0.182, F=29.640, p=0.032), up to the middle of the century. From that moment on, proportions fluctuated. Only after 1880 could the use of poison be assessed.

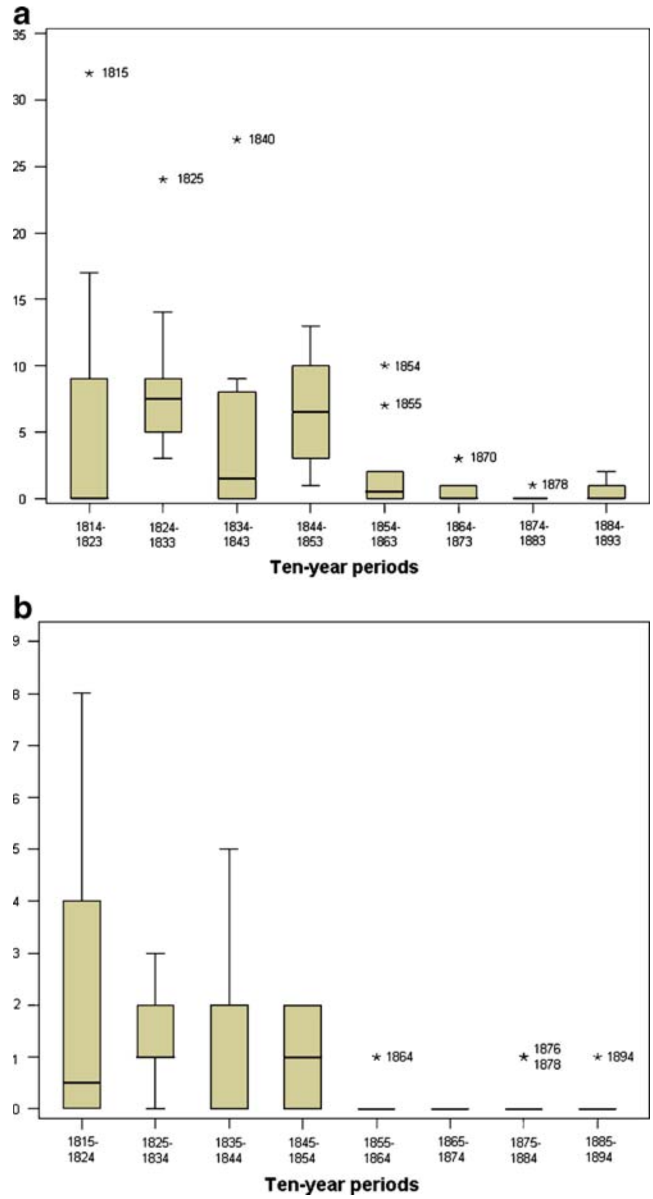

Fig. 1 Annual number of adult and young wolves (1814–1893, **a** *above*) and litters (1815–1894, **b** *below*) recorded in 10-year periods. Median (*thick bar*), interquartile range (*box*), range to the highest and lowest values within 1.5 interquartile ranges (*whiskers*), and outliers are shown for each time period

Trend in litters captured in dens

During 1815–1894, we found 59 records in which pups were mentioned, thus corresponding to captured litters (X_{year}=0.58, s=1.39, max=4, min=0), totalizing 257 individual pups. Although bounties for adult wolves remained in force over a

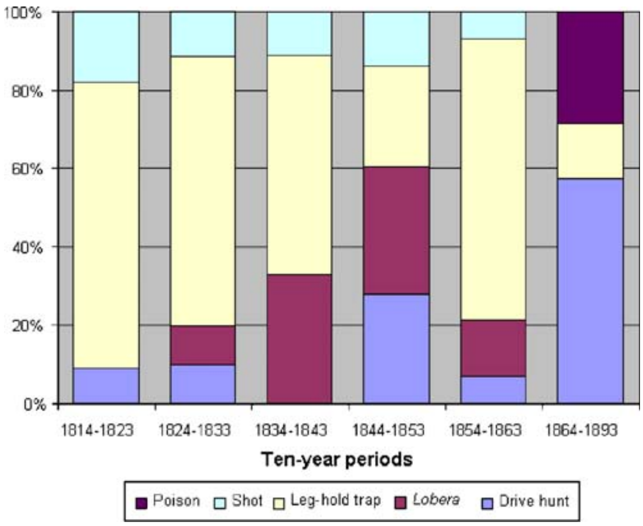

Fig. 2 Percentage of frequencies of adult and young wolves killed by different hunting methods per 10-year periods, between 1814 and 1893. The last three periods were merged together. Number of wolves assessed for each period were 22 (1814–1823), 61 (1824–1833), 18 (1834–1843), 43 (1844–1853), 14 (1854–1863), and 7 (1864–1893)

longer period, the last litter was recorded in 1894. By grouping records for 10-year periods, a shift was observed again between 1815–1854 and 1855–1894, when litter captures became extremely scarce (Fig. 1).

Age ratio

The global age ratio (pups/adults and young) was 0.83 (257:308) for the period 1805–1905. By selecting the series of years with pups recorded (1815–1894), both variables showed a statistically significant association (r_s=0.529, p> 0.001, n=80; data without bivariate normal distribution, Kolmogorov–Smirnov test). After grouping data on a 10-year basis (Table 1), it was observed that the age ratio decreased progressively, though it suffered fluctuations during the last two periods.

Sex ratio

During the period 1805–1905, 168 males and 140 females (ratio 1.19) included in the “adults and young” age class were recorded. When 10-year periods between 1814 and 1893 were examined, the proportion of males showed an upward trend (Table 2).

Litter size

The average size of litters was 4.36 (s=2.60, max=13, min=1, n=59). Litters with just one pup were the most common (17.5%), but the frequencies of each size, 1 to 5, reached similar values and formed as a whole about 70.2% of the records. The annual average litter size on a 10-year basis decreased around mid-century and increased later (Fig. 3).

Spatial distribution of mortality

The annual average density of adults and young wolves killed in the study area, deduced from provincial archives, was 0.04 wolves/100 km^2 for the period 1814–1905. Nonetheless, the spatial distribution of the bag was not regular. The harvest density model helped to identify three main continuous ranges (Fig. 4): north-western, western, and eastern. As for litters taken, the annual average during the period 1815–1894 for records extracted from provincial archives was 0.01 litters/100 km^2. The distribution model identified three distinct breeding ranges: north-western, central, and eastern (Fig. 4). Interestingly, the western adult range provided no record of litters taken.

Seasonal distribution of adult and young mortality

The monthly distribution of frequencies (n=298) showed that hunting pressure on adults and youngsters was mainly exerted in winter (November–March, 73.5%), with a reduction in spring and autumn (April–May and September–October, 20.8%) and especially in summer (June–August, 5.7%). Though a seasonal influence seemed to exist on the type of non-natural mortality, with a predominance of leg-hold trapping during the winter months and a relative increase in drive hunts in spring and autumn, a statistically significant association between both variables (χ^2 test of independence grouping the cases on a two-monthly basis, df=8, p=0.07) could not be established. The two-way ANOVA with replication (Table 3) showed that the level of mortality was influenced both by season and by hunting method, but in addition, the two factors interacted so that each type of mortality shifted its importance temporarily. The effect of seasonal variation was more pronounced in mortality by leg-hold traps than by drive hunts (Fig. 5).

Data from municipal archives

Records of 237 wolves killed in the period 1693–1804 were compiled (X_{year}=2.2 wolves, s=2.46, max=13, min=0), and 42 in the period 1813–1841 (X_{year}=1.4 wolves, s=1.95, max=9, min=0), mostly without reference to age, sex, or location, although 14 additional records of litters were explicitly mentioned. We took the broadest continuous available series (1693–1804, a 112-year span) to detect a possible cyclic pattern with spectrum density analysis (smoothed of Tuckey–Hamming to eliminate irregular

Table 1 Age ratio and annual average on a 10-year basis

10-year periods	Age ratio (pups/adults and young)	Number of pups	Number of adults and young	Age ratio annual average	*s*
1815–1824	1.66	108	65	1.02	0.95
1825–1834	0.75	58	77	0.82	0.69
1835–1844	0.56	36	66	0.46	0.93
1845–1854	0.53	33	62	1.51	3.07
1855–1864	0.27	3	11	0	
1865–1874	0	0	7	0	
1875–1884	10	10	1	0	
1885–1894	1.50	9	6	0	
Global 1815–1894	0.88	257	293	0.90	1.96

variation, extent 3). Short- and long-term (cyclic) oscillations were revealed (Fig. 6). Annual wolf and red fox records were plotted and lineal regressions with 95% confidence interval carried out on the period when wolf and red fox bounties were in force simultaneously in the study area (1726–1841; Fig. 7).

Discussion

Degree of consistency of data sources

As in every piece of archive research, the eventual partiality of records can obscure the detection of spatial and temporal patterns in mortality (Riley et al. 2004). Other demographic studies that have used archive data were forced to complete and normalize their series by means of regression (Jedrzejewska et al. 1996; Alcántara and Cantos 1992; Torrente 1999). In our datasets, it was initially assumed that the number of records in provincial archives closely matched the actual number of kills. Checking provincial archive numbers against municipal ones, with regard to the overlap period (1813–1841), supported this view, as few additional records could be detected.

Wolf hunting pressure probably remained constant in the study area. First, according to bounties issued by municipal councils during 1726–1841, the number of wolves decreased ($r=-0.13$, $p=0.18$), while that of red foxes tended to increase ($r=0.09$, $p=0.37$). In Biscay (a province that accounts for one third of the study area), during 1814–1815, 38.3 foxes/100 km^2 (including adults and pups) were hunted, whereas in 1864–1865 they numbered 61.1 (Junta General de Estadística 1865; Fernández and Ruiz de Azua 2003). This suggests that the activity of professional and part-time hunters did not diminish, either as a result of a compensatory shift between the species that provided the main incomes, or as a consequence of an increase of fox population, due to the absence of top predators. Second, if the approved tariffs are taken into account, the bounties granted by the provincial councils remained fairly constant during most of the nineteenth century, as did economic incentives for hunters, compared with other sources of income in rural society (Torrente 1999). So, we assume that such circumstances did not distort our data, unlike the case presented by Joly and Messier (2000) relating to the wolf pelt prize and wolf harvest in Canada. Besides, any distortion could have been compensated by an increase in collective drive hunts,

Table 2 Sex ratio on a 10-year basis and statistical significance associated with the probability of a χ^2 test

10-year periods	Sex ratio (males/females)	Number of males	Number of females	χ^2
1814–1823	0.71	25	35	0.197
1824–1833	1.20	49	41	0.399
1834–1843	1.35	31	23	0.258
1844–1853	0.91	31	34	0.426
1854–1863	2.50	15	6	0.050
1864–1873	6	6	1	0.059
1874–1883		1	0	0.317
1884–1893		6	0	0.005
Global 1814–1893	1.17	164	140	0.169

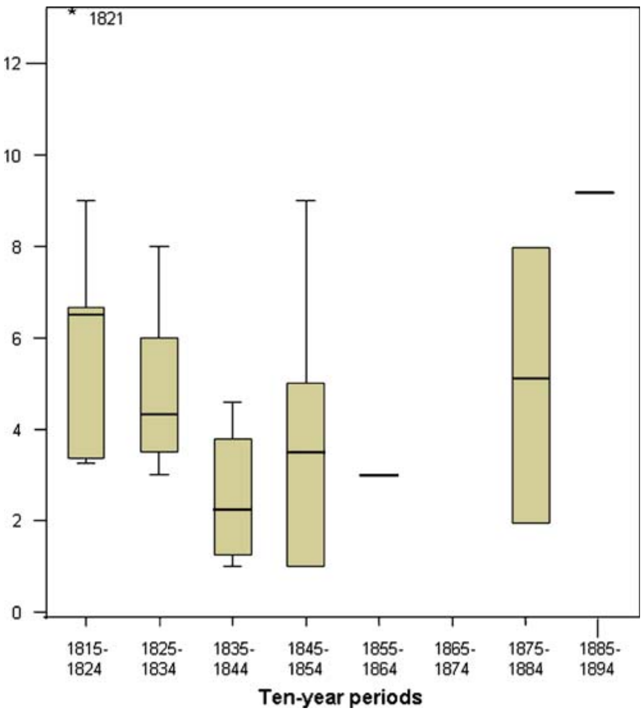

Fig. 3 Variation in annual average of litter sizes on a 10-year basis (1815–1894). Median (*thick bar*), interquartile range (*box*), range to the highest and lowest values within 1.5 the interquartile ranges (*whiskers*), and outliers are shown for each time period. Number of litters recorded for each period were 22 (1815–1824), 13 (1825–1834), 11 (1835–1844), 9 (1845–1854), 1 (1855–1864), 0 (1865–1874), 2 (1875–1884), and 1 (1885–1894)

Table 3 Results of a two-way ANOVA with replication about the influence of factors “cause of mortality” (leg-hold trap, drive hunt, or shooting) and “seasonality” (bimonthly)

Factor	*df*	SS	MS	*F*	*p*
Cause of mortality	2	198.5	99.25	15.27	<0.001
Seasonality (bimonthly)	5	314.7	62.93	9.68	<0.001
Interaction	10	244.8	24.48	3.77	0.007
Error	18	117	6.50		

a method more suited to the progressively rarer presence of wolves (Mech 1981).

A last point relates to the temporal discontinuity of files in provincial archives. The lack of reports before 1813 and during the period 1835–1837 is explained by the absence of administrative stability during war periods that affected the study area. We conclude that hunting pressure was interrupted because simultaneous research in municipal council archives did not render records for either of those periods, and the combined reasons of a lack of bounties and a ban on fire arms should reasonably prevent persecution (as actually conveyed by contemporary texts). The recovery of wolf populations as a consequence of hunting ceasing during periods of unrest has occasionally been reported (Grande del Brío 1984; Butzeck et al. 1988; Gutiérrez 2005), and our data are coherent with that. The alternative option of an increase in persecution after periods of war is dismissed because we found a lag of years

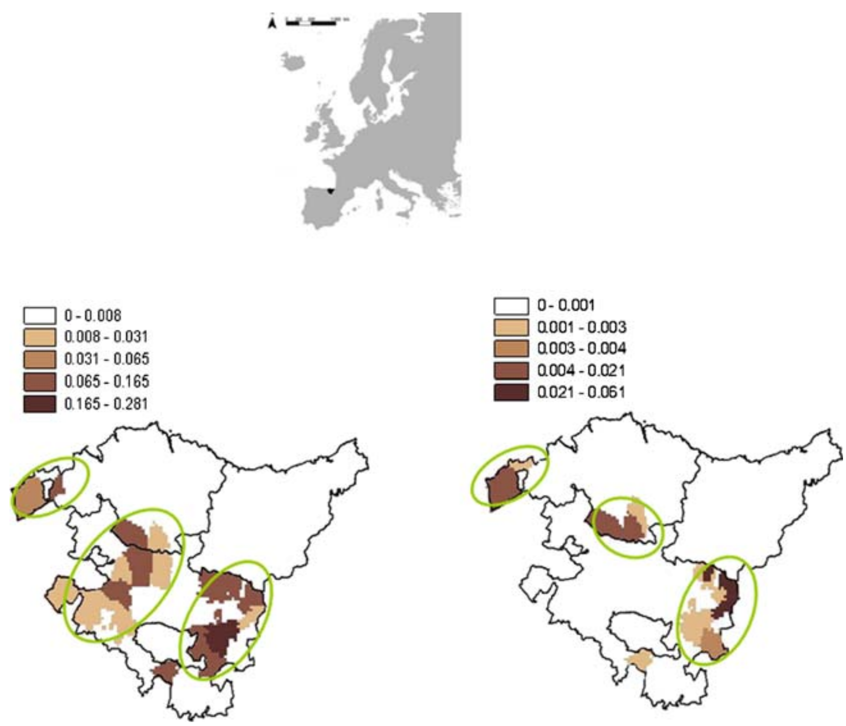

Fig. 4 Models for density of records concerning adult and young wolves (*left*) and litters (*right*), developed with assign proximity function implemented in spatial analysis module in Arcview 3.2 (raster image with 1 km side pixels). Intervals were obtained with natural breaks algorithm (Jenk’s optimization method to minimize sum of variance within each class). Areas with apparent spatial continuity are delimited

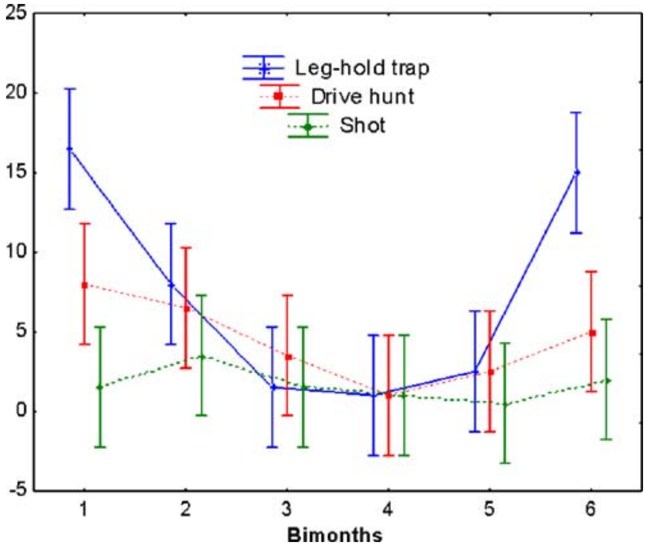

Fig. 5 Interacting effect between "cause of mortality" (leg-hold trap, drive hunt, and shooting) and "seasonality" (bimonthly) over average number of hunting records of adult and young wolves (95% confidence intervals)

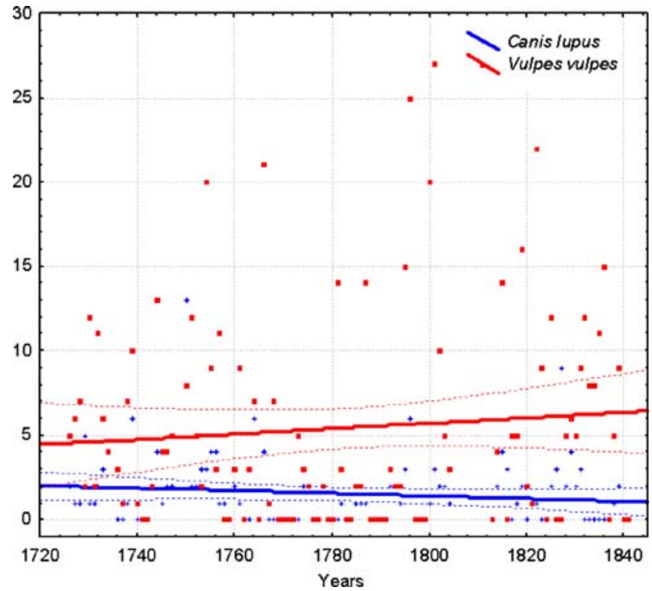

Fig. 7 Lineal regressions and 95% confidence intervals for wolf and red fox records, compiled in account books from Urcabustaiz municipal archive, during the period 1726–1841

between the resumption of bounties and the observation of the highest bags, relative to a delayed numerical response as noted in some wolf populations (Sidorovich et al. 2003).

Human persecution or food stress? Demographic insights

The progressive increase in the male/female wolf ratio in the time series may be a consequence of an increasing shortage in trophic resources or, alternatively, the result of immigration processes in the context of a non-saturated population. As for the first of these explanations, Mech (1981) proposed differential competitive ability favoring males in wolf populations under social or food stress, responsible for a sex ratio deviation, and rejected sex-influenced trappability. Moreover, the higher economic

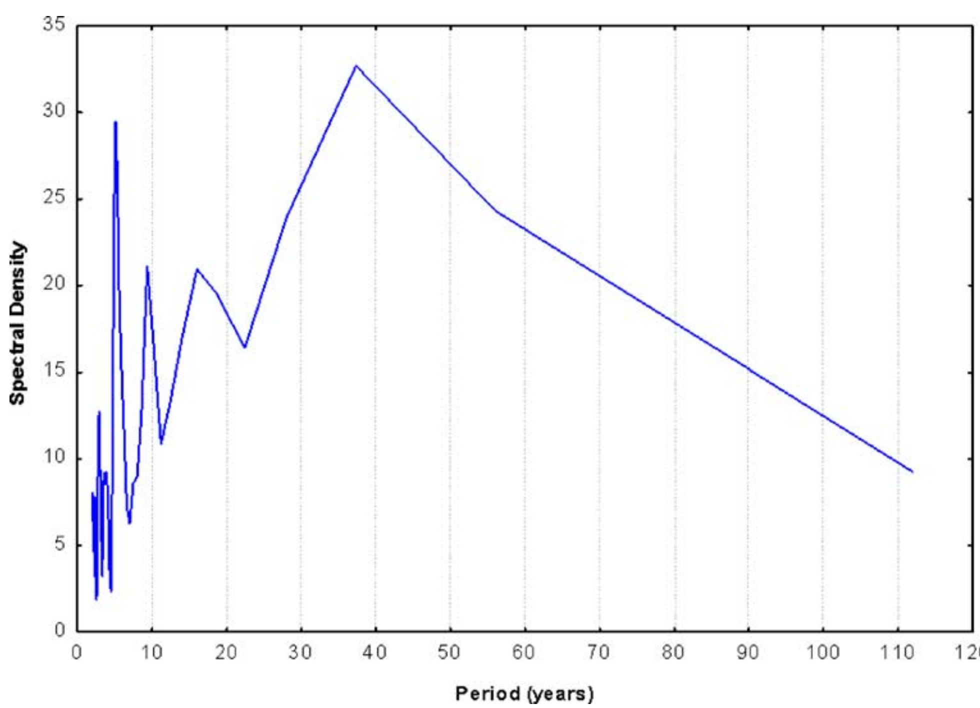

Fig. 6 Spectral density for the time series of adult and young wolves (1693–1804), showing long-term oscillation around 35 years

value of females should induce constant overrepresentation in archive records. The explanation justifying the second interpretation would be that dispersal is influenced by sex in wolf populations, which has been suggested in some cases of resettlement (Wabakken et al. 2001), but not as a general rule (Fuller 1989; Gese and Mech 1991; Huber et al. 2002). As for dispersing wolves hunted in the study area during 1987–1997 (n=24) and those sexed in 2003–2004 by molecular analysis from scat samples (n=12), there were no deviations favorable to males either (Sáenz de Buruaga et al. 2000; Echegaray et al. 2007).

On the other hand, the diminishing trend in age ratio and litter size does not tally with the expected increases in a population which is regulated by means of hunting and which has enough food resources (Fuller et al. 2003). Increases in the proportion of breeding females and in litter size are the main compensatory mechanisms verified in exploited populations (Fuller 1989; Messier 1995; Mech et al. 1998; Mech 1981). Litter size depends mainly on pup survival because the number of fetuses per pregnant female seems to be quite a stable parameter (Mech 1981; but see Fuller and Sievert 2001). In this way, Harrington et al. (1983) proposed that the reduction of pup survival during the rearing period—and not young or subadult dispersal—is the outstanding piece of evidence for trophic stress in wolf populations, and Espuno (2004) observed a decrease in pack size in French Mercantour wolf population as a consequence of wild ungulate vigilance and livestock protection. This variable is therefore the most sensitive to per capita food availability (Harrington et al. 1983; Fuller et al. 2003).

Role of poisoning

Poison is regarded as the most effective method for the eradication of wolf populations (Mech 1981; Boitani 2003). Only two late records were gathered concerning poisoned wolves and just one reference in the bibliographic review relative to the nineteenth century and the study area (Múgica 1895). We reject a possible underestimation of poisoning because the use of strychnine in northern Spain was not common before 1880 (Dirección General de Agricultura, Industria y Comercio 1861; Grande del Brío 1984; Valverde and Teruelo 2001). It could be argued that the carcasses of poisoned wolves were not easily recovered and not taken for bounty. Nevertheless, archive reports often show how hunters made great efforts to find wolves that had been wounded and had escaped, so one can deduce that the bounty was sufficiently attractive, in a similar way, to warrant searching for poisoned wolves (Múgica 1895). Therefore, we conclude that poisoning does not appear to be a determining factor in wolf population decline in the study area during most of the nineteenth century.

Prey availability

The gradual fragmentation of roe deer distribution in the study area and its extinction around the last decades of the nineteenth century are well established from records published in Madoz's dictionary (1845–1850) and other documents (Markina 2000). The decline in the range of the wild boar (*Sus scrofa*) was also sharp, although a few individuals persisted in remote corners of the study area. This species probably played a minor role in the Iberian wolf's diet, quite unlike the roe deer, as deduced from current food habits (Salvador and Abad 1987; Vilá et al. 1990; Cuesta et al. 1991; Fernández 2004), and no spatial correlation between the evolution of boar and wolf numbers over time has been detected in Spain (Nores et al. 1995).

As for livestock in the study area, the reports available from the Statistical Yearbook of Spain (Junta General de Estadística 1865, 1915) provide evidence for a numerical collapse during the last third of the nineteenth century (loss of 64% of the sheep herd, 43% of goats, 25% of horses, and 17% of cattle), as a consequence of a severe crisis in the livestock sector and the wool market especially (Alberdi 2003). Although the relevance of domestic ungulates in the wolf's trophic ecology may be conditioned by husbandry ("theory of vulnerable prey biomass" in Mech and Peterson 2003; see Meriggi and Lovari 1996; Nowak et al. 2005; Berger 2007), the reduction in livestock numbers must have had a negative influence on their consumption by wolves.

The trophic adaptability of the species allows it to overcome temporal reductions in the availability of ungulates (Boitani 2003), but the existence of abundant secondary prey is a requisite (Okarma 1995; Chavez and Gese 2005). Food habits of current Iberian populations are based on wild ungulates or livestock (Cuesta et al. 1991; Vos 2000; Blanco 2001), and although there are some living mainly on rabbits (*Oryctolagus cuniculus*), this is not the case in northern Spain, where this prey is very scarce in the wild. Carcasses discarded from intensive livestock farms also provide trophic resources for such populations, but carrion dumps associated with this modern farming system had obviously not yet been developed in the nineteenth century, with the result that few alternative resources would have been available.

Wolf populations in remote zones without human interference are subject to natural fluctuations relating to predator–prey dynamics (Mech et al. 1998, but see Oksanen et al. 2001). In Europe, cycles have rarely been indicated (Johnson 2004), despite their practical interest for the evaluation of censuses and conservation status within a given temporal frame (Blanco and Cortés 2002). Non-natural cycles have been studied for the dingo (*C. lupus dingo*), determined by food abundance in source areas and dispersal into humanized and sink areas, where mortality is higher (Thomson et al. 1992). Our data series for the eighteenth century could also be interpreted as suggesting the existence of long-term fluctuations in this exploited population.

Dispersal and spatial dynamics

From the spatial perspective, the population of wolves in the study area was not isolated within the Iberian range, but immigration could not prevent extinction—as generally proposed (Liberg et al. 2005)—possibly because similar processes were operating in neighboring areas (Rico and Torrente 2000). The flow of dispersing wolves—mainly youngsters and subadults between 1 and 3 years old—tends to connect saturated zones with others having more trophic resources or lower wolf density. Some records were found in municipalities far from the core breeding areas suggesting movement of dispersing wolves. But, we could not obtain this type of data after 1826, a circumstance that would be consistent with a population showing a gradual easing of intraspecific competition under conditions of low density and productivity, allowing vagrants to remain in the proximities of parental territories (Messier 1985; Potvin 1987; Gese and Mech 1991; Meier et al. 1995; Ballard et al. 1997; Mech et al. 1998; Fuller et al. 2003).

Seasonal and local variations in persecution techniques are attested. The former relate to the use of leg-hold traps, the method selected by professional hunters, and the latter to the exclusive use of *loberas* at the western end of the study area (Álvares et al. 2000). The higher efficiency of communal hunting systems is suggested by the weaker relative persistence of the population in this sector, since no breeding data have been found. Moreover, from 1862 on, every wolf kill recorded occurred outside this western area. The dynamics of wolf populations is more sensitive to adult survival than to that of the young or breeding output (Chapron et al. 2003).

Conclusion

Modeling the viability of wolf metapopulations in fragmented landscapes (concept reviewed by Linnell et al. 2007) suggests that a negative long-term trend in the availability of prey greatly increases the probability of extinction (Haight et al. 1998; Vucetich et al. 1997). In Russian Karelia, the joint analysis of a time series (35 years) of abundance of moose (*Alces alces*) and hunting pressure on a wolf population in decline showed the primary influence of prey biomass on pup productivity and survival, increasing the vulnerability of the population confronted with a rate of extraction that was kept at a constant level (Kojola and Danilov 2001). In Belarus, the functional response of wolves to a brief shortage in the biomass of wild ungulates was an increased predation on livestock (Sidorovich et al. 2003), and no numerical response was noticed. We conclude that a similar interpretation may be coherent with the historical information presented here, suggesting that long-term food reduction could play a more substantial role in the decline of wolf populations under persecution than has usually been recognized by short-term studies.

Acknowledgments The authors thank Francisco J. Purroy, Carles Vilà, Bogumila Jedrzejewska, Jorge Echegaray, Arturo Menor, Eugenio Murguía, Miguel Ángel Campos, Mario Sáenz de Buruaga, Teresa Andrés, Brian Webster, Nick Gardner, and the officials at Archivo del Territorio Histórico de Álava, Archivo Histórico Foral de Vizcaya, and Archivo General de Guipúzcoa for their kind assistance.

References

Alberdi JC (2003) Políticas agroambientales y ganadería en los montes de utilidad pública del País Vasco. Pap Geogr 38:5–26

Alcántara M, Cantos FJ (1992) Tendencias históricas de la comunidad de carnívoros del Monte de El Pardo (Madrid, España central). Misc Zool 16:171–178

Álvares F, Alonso P, Sierra P, Petrucci-Fonseca F (2000) Os fojos dos lobos na Península Ibérica. Sua inventariaçao, caracterizaçao e conservaçao. Galemys 12:57–77

Andersen R, Linell JD, Solberg EJ (2006) The future role of large carnivores on terrestrial trophic interactions: the northern temperate view. In: Danell K, Bergström R, Duncan P, Pastor J (eds) Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, Cambridge, pp 413–448

Aragón Á (2003) Gestión, uso y aprovechamiento de comunales y parzonerías en la Edad Moderna: el ejemplo de Entzia y de Urbia. In: Pastor E (ed) La Llanada oriental a través de la historia. Diputación Foral de Álava, Vitoria, pp 81–91

Ballard WB, Ayres LA, Krausman PR, Reed DJ, Fancy SG (1997) Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildl Monogr 135:5–47

Beaufort E (1987) Le loup en France. Elements d'ecologie historique. SFEPM, Paris

Berger J (2007) Carnivore repatriation and holarctic prey: narrowing the deficit in ecological effectiveness. Conserv Biol 21:1105–1116

Blanco JC (2001) El hábitat del lobo: la importancia de los aspectos ecológicos y socioeconómicos. In: Camprodon J, Plana E (eds) Conservación de la biodiversidad y gestión forestal. Universitat de Barcelona, Barcelona, pp 415–431

Blanco JC, Cortés Y (2002) Ecología, censos, percepción y evolución del lobo en España: análisis de un conflicto. Sociedad Española para la Conservación y Estudio de los Mamíferos, Málaga

Blanco JC, Reig S, Cuesta L (1992) Distribution, status and conservation problems of the wolf *Canis lupus* in Spain. Biol Conserv 60:73–80. doi:10.1016/0006-3207(92)91157-N

Boitani L (2003) Wolf conservation and recovery. In: Mech LD, Boitani L (eds) Wolves. Behaviour, ecology and conservation. University of Chicago Press, Chicago, pp 317–340

Boitani L, Asa C, Moehrenschlager A (2004) Tools for canid conservation. In: Macdonald DW, Sillero-Zubiri C (eds) Biology and conservation of wild canids. Oxford University Press, Oxford, pp 143–159

Butzeck S, Stubbe M, Piechocki R (1988) Beiträge zur Geschichte der Säugetier-fauna der DDR. Der Braunbär *Ursus arctos* Linné 1758. Hercynia 25:27–59

Carrete M, Grande JM, Tella JL, Sánchez JA, Donázar JA, Díaz R, Romo A (2007) Habitat, human pressure, and social behavior: partialling out factors affecting large-scale territory extinction in an endangered culture. Biol Conserv 136:143–154. doi:10.1016/j.biocon.2006.11.025

Caussimont G (1981) Le loup en Navarre (XVIII-XIX s.) et les dernières campagnes de destruction dans les Pyrénées occidentales. Acta Biol Montana 1:81–92

Chapron G, Legendre S, Ferrière R, Clobert J, Haight RG (2003) Conservation and control strategies for the wolf (*Canis lupus*) in Western Europe based on demographic models. C R Biol 326:575–587. doi:10.1016/S1631-0691(03)00148-3

Chatfield C (2003) The analysis of time series: an introduction. Chapman and Hall, London

Chavez AS, Gese EM (2005) Food habits of wolves in relation to livestock depredation in Northwestern Minnesota. Am Midl Nat 154:253–263. doi:10.1674/0003-0031(2005)154[0253:FHOWIR]2.0.CO;2

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

Dirección General de Agricultura Industria y Comercio (1861) Apuntes relativos a la aparición y extinción de animales dañinos en las provincias del Reino. Ministerio de Fomento, Madrid

Echegaray J, Illana A, Hernando A, Martínez de Lecea F, Bayona J, Covela I, De la Torre Á, Paniagua D, Vilá C (2007) Uso de técnicas genéticas no invasivas para estimar el tamaño y la distribución del lobo (*Canis lupus* Linnaeus, 1758) en el País Vasco (N España). Galemys 19(2):3–18

Elgmork K (1996) Historic review of brown bears and wolves in central-south Norway: 1733–1845. Fauna Oslo 49:134–147

Espuno N (2004) Impact du loup (*Canis lupus*) sur les ongulés sauvages et domestiques dans le Massif du Mercantour. Université Montpellier II, Montpellier

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

Fernández JM, Ruiz de Azua N (2003) Notas históricas sobre algunas especies faunísticas. In: Fernández JM (ed) Estudio faunístico del Parque Natural del Gorbeia. Diputación Foral de Álava, Vitoria, pp 35–81

Fuller TK (1989) Population dynamics of wolves in north-central Minnesota. Wildl Monogr 105:1–41

Fuller TK, Mech LD, Cochrane JF (2003) Wolf population dynamics. In: Mech LD, Boitani L (eds) Wolves. Behaviour, ecology and conservation. University of Chicago Press, Chicago, pp 161–191

Fuller TK, Sievert PR (2001) Demography and the consequences of changes in prey availability. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) Carnivore conservation. Cambridge University Press, Cambridge, pp 61–92

Garayo JM (1992) Los montes del País Vasco (1833–1935). Agric Soc 65:121–174

Gese EM, Mech LD (1991) Dispersal of wolves (*Canis lupus*) in Northeastern Minnesota, 1969–1989. Can J Zool 69:2946–2955

Grande del Brío R (1984) El lobo ibérico. Biología y mitología. Hermann Blume, Madrid

Grau JM, Puig R, Ruiz-Olmo J (1990) Persecución del lobo (*Canis lupus* L., 1758) en Girona (NE ibérico) durante los siglos XVIII y XIX: ejemplo de utilización de datos de archivo. Misc Zool 14:217–223

Green RE (2002) Diagnosing causes of population declines and selecting remedial actions. In: Norris K, Pain KJ (eds) Conserving bird biodiversity. Cambridge University Press, Cambridge, pp 139–156

Gutiérrez V (2005) El lobo ibérico en Andalucía. Junta de Andalucía, Sevilla

Haight RG, Mladenoff DJ, Wydeven AP (1998) Modeling disjunct gray wolf populations in semi-wild landscapes. Conserv Biol 12:879–888. doi:10.1046/j.1523-1739.1998.97103.x

Harrington FJ, Mech LD, Fritts SH (1983) Pack size and wolf pup survival: their relationship under varying ecological conditions. Behav Ecol Sociobiol 13:19–26. doi:10.1007/BF00295072

Huber D, Kusak J, Frkovic A, Guzvica G, Gomercic T (2002) Causes of wolf mortality in Croatia in the period 1986–2001. Vet Arh 72:131–139

Jedrzejewska B, Jedrzejewski W, Bunevich AN, Milkowski L, Okarma H (1996) Population dynamics of wolves *Canis lupus* in Bialowieza primeval forest (Poland and Belarus) in relation to hunting by humans, 1847–1993. Mamm Rev 26:103–126. doi:10.1111/j.1365-2907.1996.tb00149.x

Johnson WE (2004) Evaluating and predicting the impact of exploitation and trade on canid populations. In: Sillero-Zubiri C, Hoffman M, Macdonald DW (eds) Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan. IUCN, Gland, pp 267–272

Joly D, Messier F (2000) A numerical response of wolves to buffalo abundance in Wood Buffalo National Park. Can J Zool 78:1101–1104

Junta General de Estadística (1865) Anuario estadístico de España 1862–1865. Imprenta Nacional, Madrid

Junta General de Estadística (1915) Anuario estadístico de España 1915. Imprenta Nacional, Madrid

Kojola I, Danilov PI (2001) Wolf population dynamics in Eastern Fennoscandia: does human exploitation mask the effects of prey density? Canid Biology and Conservation International Conference. IUCN Canid Specialist Group, Oxford, p 38

Liberg O, Andrén H, Pedersen HC, Sand H, Sejberg D, Wabakken P, Akesson M, Benshc S (2005) Severe inbreeding depression in a wild wolf (*Canis lupus*) population. Biol Lett 1:17–20. doi:10.1098/rsbl.2004.0266

Linnell JD, Nilsen EB, Lande US, Herfindal I, Odden J, Skogen K, Andersen R, Breitenmoser U (2005) Zoning as a means of mitigating conflicts with large carnivore. Principles and reality. In: Woodroffe R, Thirgood S, Rabinowitz A (eds) People & wildlife: conflict or coexistence?. Cambridge University Press, Cambridge, pp 162–175

Linnell JD, Salvatori V, Boitani L (2007) Guidelines for population level management plans for large carnivores. Istituto di Ecologia Applicata, Rome

Madoz P (1845–1850) Diccionario geográfico-estadístico-histórico de España y sus posesiones de ultramar. Madrid

Markina F (2000) Estudio de las poblaciones de corzo (*Capreolus capreolus* L.) y jabalí (*Sus scrofa* L.) y análisis de su explotación cinegética en el Territorio Histórico de Álava. Universidad de León, León

Mech LD (1995) The challenge and opportunity of recovering wolf populations. Conserv Biol 9:270–278. doi:10.1046/j.1523-1739.1995.9020270.x

Mech LD (1981) The wolf. The ecology and behavior of an endangered species. University of Minnesota Press, Minneapolis

Mech LD, Adams LG, Meier TJ, Burch JW, Dale BW (1998) The wolves of Denali. University of Minnesota Press, Minneapolis

Mech LD, Boitani L (2004) Grey wolf. In: Sillero-Zubiri C, Hoffman M, Macdonald DW (eds) Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan. IUCN, Gland, pp 124–129

Mech LD, Peterson RO (2003) Wolf–prey relations. In: Mech LD, Boitani L (eds) Wolves. Behaviour, ecology and conservation. University of Chicago Press, Chicago, pp 131–160

Meier TJ, Burch JW, Mech LD, Adams LG (1995) Pack structure and genetic relatedness among wolf packs in a naturally regulated population. In: Carbyn LN, Fritts SH, Seip DR (eds) Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, pp 293–302

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

Messier F (1985) Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Can J Zool 63:239–245. doi:10.1139/z85-037

Messier F (1995) On the functional and numerical responses of wolves to changing prey densities. In: Carbyn LN, Fritts SH, Seip DR (eds) Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, pp 187–197

Mills LS (2007) Conservation of wildlife populations. Demography, genetics, and management. Blackwell, Malden

Múgica S (1895) La caza del lobo en nuestras montañas. Euskal-Erria Rev Bascongada 32:233–243

Nilsson T (2003) Integrating effects of hunting policy, catastrophic events, and inbreeding depression, in PVA simulation: the Scandinavian wolf population as an example. Biol Conserv 115:227–239. doi:10.1016/S0006-3207(03)00120-4

Nores C, González F, García P (1995) Wild boar distribution trends in the last two centuries: an example in Northern Spain. Ibex J Mt Ecol 3:137–140

Nowak S, Myslajek SW, Jedrzejewska B (2005) Patterns of wolf *Canis lupus* predation on wild and domestic ungulates in the western Carpathian Mountains (S Poland). Acta Theriol (Warsz) 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 (Warsz) 40:335–386

Oksanen T, Oksanen L, Schneider M, Aunapuu M (2001) Regulation, cycles and stability in northern carnivore–herbivore systems: back to first principles. Oikos 94:101–117. doi:10.1034/j.1600-0706.2001.11315.x

Orsini P (1996) Quelques éléments sur la disparition du loup (*Canis lupus*) en Provence au cours du XIXéme siecle. Faune Provence 17:23–31

Phillips MK, Bangs EE, Mech LD, Kelly BT, Fazio BB (2004) Grey wolves-Yellowstone. Extermination and recovery of red wolf and grey wolf in the contiguous United States. In: Macdonald DW, Sillero-Zubiri C (eds) Biology and conservation of wild canids. Oxford University Press, Oxford, pp 143–159

Potvin F (1987) Wolf movements and population dynamics in Papineau Labelle Reserve, Quebec. Can J Zool 66:1266–1273

Rico M, Torrente JP (2000) Caza y rarificación del lobo en España: investigación histórica y conclusiones biológicas. Galemys 12:163–179

Riley SJ, Nesslage GM, Maurer BA (2004) Dynamics of early wolf and cougar eradication efforts in Montana: implications for conservation. Biol Conserv 119:575–579. doi:10.1016/j.biocon.2004.01.019

Sáenz de Buruaga M, Campos MÁ, Arberas E, Onrubia A (2000) Últimos datos sobre el lobo (*Canis lupus*) en el País Vasco y Navarra. Galemys 12:149–162

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

Sidorovich V, Tikhomirova L, 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

Sillero-Zubiri C, Schwitzer D (2004) Management of wild canids in human-dominated landscapes. In: Sillero-Zubiri C, Hoffman M, Macdonald DW (eds) Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan. IUCN, Gland, pp 257–266

Thomson PC, Rose K, Kok NE (1992) The behavioral ecology of dingoes in Northwestern Australia. IV. Social and spatial organization and movements. Wildl Res 19:543–563. doi:10.1071/WR9920543

Torrente JP (1999) Osos y otras fieras en el pasado de Asturias. Fundación Oso de Asturias, Oviedo

Valverde JA, Teruelo S (2001) Los lobos de Morla. Al Andalus, Sevilla

Vilá C, Uríos V, Castroviejo J (1990) Ecología del lobo en la Cabrera (León) y la Carballeda (Zamora). In: Blanco JC, Cuesta L, Reig S (eds) El lobo (*Canis lupus*) en España. Situación, problemática y apuntes sobre su ecología. Ministerio de Agricultura Pesca y Alimentación, Madrid, pp 95–108

Vos J (2000) Food habits and livestock depredation of two Iberian wolf packs (*Canis lupus signatus*) in the north of Portugal. J Zool (Lond) 251:457–462. doi:10.1111/j.1469-7998.2000.tb00801.x

Vucetich JA, Peterson RO, Waite TA (1997) Effects of social structure and prey dynamics on extinction risk in gray wolves. Conserv Biol 11:957–965. doi:10.1046/j.1523-1739.1997.95366.x

Wabakken P, Sand H, Liberg O, Bjärvall A (2001) The recovery, distribution and population dynamics of wolves on the Scandinavian peninsula, 1978–1998. Can J Zool 79:710–725. doi:10.1139/cjz-79-4-710

Woodroffe R (2001) Strategies for carnivore conservation: lessons from contemporary extinctions. In: Gittleman JL, Funk SM, Macdonald DW, Wayne RK (eds) Carnivore conservation. Cambridge University Press, Cambridge, pp 61–92

Yalden DW (1999) The history of British mammals. T & AD Poyser, London