Population estimates, density–dependence and the risk of disease outbreaks in the Alpine ibex *Capra ibex*

C. De Danieli & M. Sarasa

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Abstract
Population estimates, density–dependence and the risk of disease outbreaks in the Alpine ibex Capra ibex.— Wildlife monitoring and the identification of factors associated with disease outbreaks are major goals in wildlife conservation. We reviewed demographic and epidemiological data for the Alpine ibex *Capra ibex* from 1975–2013 to characterize the species' abundance and distribution dynamics on a large scale. We also explored methodological bias in monitoring and analyzed the factors potentially associated with the risk of disease outbreaks. Our results revealed that the overall abundance and distribution of Alpine ibex appeared to be increasing at both national and international scales, in agreement with the IUCN's 'Least Concern' conservation status on the international scale and on the national scale for Italy, Switzerland and France. Our comparative analysis of common monitoring methods highlights the fact that abundance values from counts are underestimated and suggests that the Alpine ibex is more abundant than is usually reported. The appearance and persistence of disease outbreaks (*e.g.* sarcoptic mange, keratoconjunctivitis or brucellosis) are related to local ibex density and abundance. The observed correlation between the demographic growth of ibex populations and disease outbreaks suggests that the risk of epizooties may be increasing or might already be high in several populations of *Capra ibex*.

Key words: *Capra ibex*, Disease outbreak, Host density, Monitoring, Parasite transmission, Population dynamics

Resumen
Estimas de poblaciones, densidad–dependencia y riesgo de aparición de brotes de enfermedades en el íbice de los Alpes, Capra ibex.— El seguimiento de la fauna silvestre y la identificación de los factores asociados con los brotes de enfermedades son algunos de los objetivos principales de la conservación de la fauna silvestre. En el presente estudio examinamos los datos demográficos y epidemiológicos del íbice de los Alpes, *Capra ibex*, entre los años 1975 y 2013 para caracterizar la dinámica de la distribución y la abundancia de la especie a gran escala. Asimismo, analizamos los sesgos metodológicos del seguimiento y estudiamos los factores que podrían estar relacionados con el riesgo de aparición y de persistencia de brotes de enfermedades. Nuestros resultados revelaron que la abundancia y la distribución del íbice de los Alpes parecen estar aumentando tanto a escala nacional como internacional, de forma acorde con el estado de conservación de la Unión Internacional para la Conservación de la Naturaleza (UICN) de Preocupación Menor a escala internacional, y en el ámbito nacional para Italia, Suiza y Francia. Nuestro análisis comparativo de los métodos convencionales de seguimiento pone de relieve el hecho de que los valores de abundancia obtenidos a partir de los conteos son infravaloraciones y sugiere que el íbice de los Alpes es más abundante de lo que se suele registrar. La aparición y la persistencia de los brotes de enfermedades (p. ej. la sarna sarcóptica, la queratoconjuntivitis o la brucelosis) están relacionadas con la densidad y la abundancia del íbice a escala local. La correlación observada entre el crecimiento de las poblaciones de íbice y los brotes de enfermedades sugiere que el riesgo de padecer epizootias podría estar creciendo o ser ya elevado en varias poblaciones de *Capra ibex*.

Palabras clave: *Capra ibex*, Brote de enfermedades, Densidad del hospedador, Seguimiento, Transmisión de parásitos, Dinámica de poblaciones

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Cédric De Danieli, Fédération Départementale des Chasseurs de la Haute–Savoie, Impasse des Glaises 74350 Villy–le–Pelloux.– Mathieu Sarasa, Fédération Nationale des Chasseurs, 13 rue du Général Leclerc 92136, Issy les Moulineaux, France.

Corresponding author: M. Sarasa. E–mail: msarasa@chasseurdefrance.com, mathieusar@hotmail.com

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Introduction

The genus *Capra* includes flagship species living in rupicolous and mountain environments that were the subject of conservation, reintroduction and management programs during the past century (Stüwe & Nievergelt, 1991; Pérez et al., 2002). *Capra ibex,* known as the Alpine ibex due to its distribution (Sarasa et al., 2012), is a good example of this phenomenon. This species is present in the wild in at least six countries (Italy, Switzerland, France, Austria, Germany and Slovenia) and national reports from Italy and France reveal that its abundance and distribution is increasing (Apollonio et al., 2009; Corti, 2012). It was threatened by extinction at the beginning of the twentieth century but today is found in numerous colonies that are occasionally exposed to risk of disease outbreaks (Couturier, 1962; Gauthier et al., 1991; Stüwe & Nievergelt, 1991; Apollonio et al., 2009).

The improvement of wildlife monitoring and the identification of factors associated with disease outbreaks in animal populations are major goals in wildlife management and conservation (Lloyd–Smith et al., 2005; Putman et al., 2011). Nevertheless, the understanding of potential associations between the demography of host species and the causes of disease outbreaks (*e.g.* introduction, spread and persistence) is hampered by limited availability of data (Lloyd–Smith et al., 2005). The investigation of the potential correlation between host demography and epidemiology is of crucial interest for wildlife biologists aiming to conserve wild animal populations. Such research can aid in the identification of key factors regarding the compatibility —defined as a population's predisposition as a suitable environment for potential outbreaks (Combes, 2001)— to disease outbreaks on a population scale.

Several reviews of the recovery process and abundance of this ibex have been published (Couturier, 1962; Shackleton, 1997), and a number of national–wide reports on ibex populations have recently appeared highlighting increasing trends in Italy and France (Apollonio et al., 2009; Corti, 2012). Nevertheless, a novel synthesis of the management challenges facing the Alpine ibex populations on an international scale could help improve knowledge of the current status of the species and lead us to reassess the potential links between ibex demography and the risk of outbreaks of diseases such as sarcoptic mange, keratoconjunctivitis, and brucellosis.

Our first objective was to review the most recent demographic data to test the hypothesis that both the overall abundance and distribution of Alpine ibex are increasing on an international scale. In light of information contained in national reports (Apollonio et al., 2009; Corti, 2012), we also expected to observe an improvement in populations on a European scale.

The second objective was to assess the accuracy of abundance estimates and methodological limits. All evaluations of species abundance are conditioned by the inherent difficulties involved in monitoring wildlife populations. Although other methods such as capture–mark–recapture (CMR) have been tested, counts (or censuses) performed in different seasons (depending on the population in question) are the most commonly used method for population estimates of the Alpine ibex (Toïgo et al., 2007; Apollonio et al., 2009; Guerra, 2010; Corti, 2012). Direct and indirect counts of ungulates have been reported in different environments (*e.g.* African forests and the boreo–nemoral zone on the west coast of Norway) but seem to be poor for predicting population changes below 10–50% (Plumptre, 2000; Mysterud et al., 2007). Nevertheless, as counts are still frequently used in the long–term monitoring of Alpine ibex (regardless of the population size and season) and, before any detailed analysis of the available data was carried out, we explored potential methodological biases. In line with previous estimates for this species (Gaillard et al., 2003; Largo et al., 2008; Giordano et al., 2012), we expected to find underestimated values in (1) census–based estimates *vs*. CMR estimates and in (2) summer censuses *vs.* winter censuses.

The third objective was to explore the factors potentially associated with the risk of disease outbreak in the Alpine ibex. Previous studies of *Capra* species have highlighted the fact that disease may be a strong destabilizing factor in population dynamics or even a conservation threat for *Capra* populations around the world (Couturier, 1962; Vyrypaev, 1985; Pérez et al., 2002). Epidemiological models predict that host density and local population size will be key factors controlling the transmission dynamics of infectious diseases (Anderson & May, 1979; Lloyd–Smith et al., 2005). The demographic characteristics of populations may determine host group size (Patterson & Ruckstuhl, 2013), for instance, and may set the threshold for successful parasite invasion and/or persistence (Lloyd–Smith et al., 2005; Jansen et al., 2012). We tested for potential links between host demography (density and population size) and the characteristics of disease outbreak (appearance and persistence).

Material and methods

Demographic data

Demographic and distribution data were compiled from scientific publications and official reports from institutions involved in the monitoring and management of Alpine ibex (table 1). We searched for data from all the countries in which Alpine ibex exist in the wild (Italy, Switzerland, France, Austria, Germany and Slovenia); nevertheless, most published data came from Italy, France and Switzerland. Comparisons between the different available sources enhance reliability and completeness of the compiled dataset. The name of the population, year of the population estimate, the estimated number of ibex and the estimation method used (censuses, CMR, monitoring season) were entered into a specially constructed database. The distribution of each colony or population was recorded using ArcGIS (ver. 10.1).

Table 1. Sources consulted for constructing the demographic dataset for Alpine Ibex *Capra ibex.*

Tabla 1. Fuentes consultadas para recopilar el conjunto de datos demográficos relativo al íbice de los Alpes, Capra ibex.

Italy
Gauthier et al. (1991); Bassano & Peracino (1992); Terrier & Rossi (1994); Weber (1994); Shackleton (1997); Mustoni et al. (2000); Dupré et al. (2001); Carlini (2004); CE.RI.GE.FA.S (2004); Dematteis et al. (2004); Giovo (2004); Jacobson et al. (2004); Parco Nazionale dello Stelvio (2004); Rosselli & Giovo (2004); Carmignola et al. (2005); Dotta & Meneguz (2006); Federazione Italiana Parchi e Riserve Naturali (2006); Gasparo & Borziello (2006); Giovo (2006); Parco Naturale Adamello Brenta (2006); Favalli (2007); Giovo (2007); Genero (2008); Giovo (2008); Maurino et al. (2008); Parco Naturale Adamello Brenta (2008); Von Hardenberg & Bassano (2008); Apollonio et al. (2009); Borgo (2009); Carnevali et al. (2009); Comprensorio Alpino, CN2(2009), TO2(2009), TO4(2009); Favalli (2009); Perrone & Cordero di Montezelomo (2009); Scillitani et al. (2009); Ufficio Faunistico (2009); Apollonio et al. (2010); Assessorato Agricoltura e Risorse naturali (2010); Genero & Favalli (2010); Giordano (2010); Guerra (2010); Mustoni et al. (2010); Servizio Foreste e Fauna (2010); Ufficio Faunistico (2010); Assessorato Agricoltura e Risorse naturali (2011); Attanasio & Pedrotti (2011); Favalli & Genero (2011); Federazione Italiana Parchi e Riserve Naturali (2011); Ferloni (2011); Giordano (2011); Giovo (2011); Maurino (2011); Scillitani (2011); Favalli (2012); Giordano (2012); Giordano et al. (2012); Maurino (2012); Ufficio Faunistico (2012); Giordano (2013); Giovo (2013); Parco Naturale Paneveggio–Pale di San Martino (2013); Servizio Foreste e Fauna (2013); Ufficio Faunistico (2013); Giordano (2014); Giovo (2014)

Switzerland
Weber (1994); Mayer et al. (1996, 1997); Shackleton (1997); Delétraz (2002); Apollonio et al. (2009); Biebach & Keller (2009); Willisch & Neuh¡aus (2009); Imesch–Bebié et al. (2010); Office fédéral de l'environnement (2010); Marreros et al. (2011); Aeschbacher et al. (2012); Office fédéral de l'environnement (2012, 2013b)

France
Pairaudeau et al. (1977); Reydellet (1984); Esteve & Villaret (1989); Gauthier et al. (1990, 1991); Michallet (1991); Michelot (1991); Blin et al. (1994); Huboux (1993); Darinot & Martinot (1994); Heuret & Coton (1994); Profit (1995); Anselme–Martin (1996); Toïgo et al. (1996); Shackleton (1997); Profit (1999); Anthoine & Delomez (2000); Girard (2000); Gardet (2001); Delétraz (2002); Toïgo et al. (2007); Corti (2008); Delorme (2008); Maillard et al. (2010); Delorme & Garnier (2011); Parc National du Mercantour (2011); Corti (2012); Delorme (2012); ONCFS (2012a, 2012b, 2012c); Papet (2012); Parc National du Mercantour (2012); Tardy et al. (2012); Hars et al. (2013b); Papet et al. (2013); Mick et al. (2014)

Austria
Shackleton (1997); Reimoser & Reimoser (2010)

Germany
Shackleton (1997); Wotschikowsky (2010)

Slovenia
Shackleton (1997); Adamic & Jerina (2010)

Density estimates

Density estimates were rarely available in articles and reports. Moreover, density estimates are scale– and method–dependent due to factors such as the variability in the spatial distribution of ungulates and the variability of the probability of detection during surveys (Wingard et al., 2011; Suryawanshi et al., 2012). Thus, to generate a proxy for density based on available information, we divided the estimated number of ibex in a population by the distribution area of the population. This conservative approach assumes that the official reports of population estimates and distributions reflect the characteristics of the population in question despite the potential biases and poor data precision they contain (Largo et al., 2008; Wingard et al., 2011).

Disease data

Data on the occurrence of disease outbreaks were gathered from scientific publications and official reports from institutions monitoring and managing Alpine ibex populations (table 1–2). Previous studies have reported that macro– and micro–parasites have uneven and context–dependent impacts on ibex individuals and populations and may give rise to endemic or epidemic (*e.g.* outbreaks) interactions (Couturier, 1962; Hars & Gauthier, 1994). Thus, we only included disease outbreaks in our database when the host–parasite interaction was characterized as such by the authors of a publication. Moreover, the spread or the incidence of parasites does not necessarily predict the potential impact of parasites on host demography. Only a few diseases are ever associated with the occasional destabilization of ibex populations or actually have the potential —by affecting ecological, health and socio–economic factors— to jeopardize their futures. The most important diseases are sarcoptic mange (caused by *Sarcoptes scabiei*), pneumonia (for instance caused by *Mycoplasma agalactiae*) and keratoconjunctivitis (caused by *Mycoplasma conjonctivae*), although contagious agalactia, foot–rot, brucellosis and paratuberculosis are also of concern from health and socio–economic points of view (Couturier, 1962; Hars & Gauthier, 1994; Mick et al., 2014). Thus, we included in our dataset disease outbreaks that were both identified as such in previous studies and were concomitant with population decreases. We recorded the start of the outbreaks (pathogen invasion) as binary data. The persistence of the outbreaks (outbreak persistence) was the number of years it took for the epidemic to become inactive (based on previous studies) or to be no longer associated with any demographic decline. This proxy for outbreak persistence takes into account the fact that the causal agents of diseases might exhibit non–lethal or asymptomatic interactions that could be potentially widespread but not necessarily associated with any demographic impact on ibex populations (Ryser–Degiorgis et al., 2009).

Missing data inference

Previous reviews of the overall distribution and abundance of mountain ungulate have sometimes inferred missing data from previously reported estimates (Shackleton, 1997; Pérez et al., 2002). We also used this approach in the analyses focused on the descriptive characterization of the overall abundance and distribution of Alpine ibex populations. This conservative approach may underestimate population abundances and distributions in species whose populations are increasing but it can also provide robust estimates of minimum population size that are methodologically comparable with previous estimates.

We used a different approach in the analyses focused on the potential associations between demographic estimates and the occurrence of disease outbreaks. Values for all the considered factors were not available for every year. Thus, to avoid the loss of key information (in particular, of information on disease outbreaks), we performed a few (< 5%) missing–data inferences for population size and area estimates. Missing data were inferred using the predictions of linear models based on neighbouring available data. This approach is conservative and takes into account the reported dynamics of Alpine ibex populations over the past half–century, which were mainly characterized by population increases (Darinot & Martinot, 1994; Girard et al., 1998).

Connectivity between populations

The identification and delimitation of independent population units is a complex task in population ecology. As a first proxy for population units, we took the population units that for practical reasons are used by the institutions that monitor and manage ibex populations (management units) (Apollonio et al., 2009; Corti, 2012). We also looked for information on reported connections between management units in scientific publications and in official reports to build a second proxy for meta–population units that group together connected management units. We considered a connected management unit to consist of populations (1) between which individuals are recorded to move or (2) with tangent/overlapping distributions. As the required information for testing potential associations between demography and epidemiology was only available for Italy and France (see below), population groups were only identified for these countries (table 2, fig. 1). We used a conservative approach, and when potential —but unconfirmed— connections were mentioned in reports, we distinguished between populations units (*e.g.* G4–G5, G11–G13; fig. 1).

Statistical analyses

In order to focus our study on the dynamic recovery of Alpine ibex on an international scale in recent decades and to reduce potential bias from unreliable former estimations we only used data from 1975 onwards.

Count (or census) data is the commonest form of population data for Alpine ibex. Thus, the overall population abundance and distribution of Alpine ibex were first predicted using count data and generalized additive models (GAM) (Wood, 2006). For some areas, population estimates inferred from CMR procedures were also available and the overall population abundance was also estimated using this data to quantify its effect on the total abundance estimates. Studies and reports on a local scale are essential for ibex management, and review analyses should support the dissemination of such studies. Thus, to maintain the large–scale focus of our analyses, to avoid pseudoreplication, and to encourage readers to refer directly to primary sources, local estimates are not presented and the references consulted for constructing the demographic dataset are given in table 1.

Paired abundance data (count *vs*. CMR estimates; end of spring–early summer counts vs. end of autumn–early winter counts) were analyzed with Student's *t*–test for paired samples.

Long–term monitoring of epidemiology, demography and distribution was only available from Italy and France. Thus, the association between demography and disease outbreaks could only be analysed for these two countries. We analyzed the potential association between the start of disease outbreaks and the demo-

Table 2. Disease outbreaks associated with population decreases taken from the literature: Fr. France; It. Italy.

Tabla 2. Brotes de enfermedades asociados con casos de disminución de poblaciones extraídos de la bibliografía: Fr. Francia; It. Italia.

Population	Year	Disease	Reference
Bargy (Fr)	1990	Keratoconjunctivitis	Huboux et al. (1992)
	2012–2013	Brucellosis	Hars et al. (2013a) Mick et al. (2014)
Parco Nazionale Stelvio (It)	2008	Contagious ecthyma	Dervaux (2012)
Antelao–Marmarole (It)	2001	Sarcoptic mange	Carmignola et al. (2006)
Croda Rossa–Croda del Becco (It)	2003	Sarcoptic mange	Carmignola et al. (2006)
Monzoni–Marmolada (It)	2004–2006	Sarcoptic mange	Carmignola et al. (2006), Guerra (2010)
Pale di San Martino (It)	2007–2008	Sarcoptic mange	Guerra (2010)
Sella (It)	2004–2005	Sarcoptic mange	Carmignola et al. (2006), Guerra (2010)
Dolomiti Friulane (It)	2010–2012	Sarcoptic mange	Favalli (2012)
Monte Canin (It)	2010	Sarcoptic mange	Favalli & Genero (2011)
Vanoise (Fr)	1976	Pneumonia	Pairaudeau et al. (1977), Deméautis (1982)
	1983	Keratoconjunctivitis	Gauthier et al. (1991), Hars & Gauthier (1994)
	2007–2011	Pneumonia/ /Keratoconjunctivitis	Delorme (2008), Parc National de la Vanoise (2009, 2010, 2011)
Parco Nazionale Gran Paradiso (It)	1976	Pneumonia	Pairaudeau et al. (1977), Gauthier et al. (1991)
	1981–1983	Keratoconjunctivitis	Gauthier et al. (1991), Hars & Gauthier (1994)
	1996–1997	Brucellosis	Ferroglio et al. (1998, 2007)
	2006–2009	Pneumonia	Delorme (2008)
Valli di Lanzo (It)	2006–2007	Pneumonia	Dotta (2009)
Tournette (Fr)	1990	Keratoconjunctivitis	Huboux (1990), Huboux et al. (1992), Hars & Gauthier (1994)

graphic factors characterizing Alpine ibex populations (density, abundance, year) using generalized additive models (GAM) and a model selection procedure based on Akaike's information criterion (Burnham & Anderson, 2002; Wood, 2006). We repeated this procedure to analyze the potential association between the persistence of disease outbreaks and factors characterizing Alpine ibex populations. In our models, we included spatial and temporal factors (population, meta–population, country, season and year).

Results

Estimated abundance

The analysis of the paired counts and CMR data ($n = 26$) revealed that counts underestimated Alpine ibex population abundance when compared to CMR protocols (mean absolute difference ± 95% confidence interval = –95 ± 27 ibex; mean relative difference = –53 ± 9%; paired *t*–test: $t = -7.22$, $P < 0.001$, df = 25).

Table 3. Meta–populations or groups of populations (G) included in the analyses of potential associations between demography and epidemiology in the Alpine ibex *Capra ibex.*

Tabla 3. Metapoblaciones o grupos de poblaciones (G) incluidas en los análisis de las posibles asociaciones entre la demografía y la epidemiología en relación con el íbice de los Alpes, Capra ibex.

G	Country	Colony name	References
G1	France	Mercantour Oriental Mercantour Occidental Cime de Tavels Aiguilles de Pélens L'Estrop Les Sagnes	Gauthier et al. (1991), Parc National Le Mercantour & Parco Naturale Alpi Marittime (2006), Apollonio et al. (2009), Corti (2012)
	Italy	Argentera Ciastella Valle Stura	
G2	France	Haute–Ubaye Saint–Ours Queyras Oriental	Rosselli & Giovo (2004), Giovo (2006), Apollonio et al. (2009), Corti (2012), Krammer (2013)
	Italy	Germanasca–Massello–Troncea Monviso–Val Pellice Parco Naturale Orsiera–Rocciavrè Valle Stura–Valle Maira	
G3	France	Cerces–Galibier	Corti (2012)
G4	France	Rochail–Muzelle	Corti (2012)
G5	France	Vieux Chaillol–Sirac	Corti (2012)
G6	France	Gorges de la Bourne Haut Plateau du Vercors	Gonin (2009)
G7	France	Belledonne	Corti (2012)
G8	France	Chartreuse	Corti (2012)
G9	France	Vanoise Encombres Champagny–Peisey Archeboc Sassière–Prariond Carro–Souces de l'Arc Dent d'Ambin	Couturier (1962), Gauthier et al. (1991), Weber (1994), Delorme (2008), Apollonio et al. (2009), Girard et al. (2009), Corti (2012)
	Italy	Gran Paradiso M. Levi–C. Vallonetto Rhêmes Rocciamelone–Lera Tersiva Valli di Lanzo	
G10	France	Tournette	Corti (2012)
G11	France	Aravis	Corti (2012)
G12	France	Sous–Dine	Corti (2012)
G13	France	Bargy	Corti (2012)
G14	France	Cornettes de Bise Arve–Giffre	Apollonio et al. (2009); Marreros et al. (2011), Office fédéral de l'environnement (2013b)
G15	France	Mont Blanc–Beaufortin	Gauthier et al. (1991), Apollonio et al. (2009), Marreros et al. (2011)
	Italy	Macugnaga–Valle Anzasca Val Veny–Gran San Bernardo Valle Antrona Valpelline–Valtournenche–Monte Rosa	

Table 3. (Cont.)

G	Country	Colony name	References
G15	Italy	Valsesia Formazza Monte Giove Premia Veglia–Devero	
G16	Italy	Alpi Lepontine V. Bregaglia–Cranna–Acqua Fraggia	Dupré et al. (2001), Apollonio et al. (2009)
G17	Italy	A. Orobie–P. 3 Signori–M. Legnone A. Orobie–Fiumenero–V. Seriana	Dupré et al. (2001), Apollonio et al. (2009)
G18	Italy	Val Malenco–Sasso di Fora–Sasso Moro Val Masino–Val di Mello	Dupré et al. (2001), Apollonio et al. (2009)
G19	Italy	Sperella–Viola–Redasco Parco Nazionale Stelvio Sesvenna Ultimo–Orecchia di Lepre	Dupré et al. (2001), Apollonio et al. (2009)
G20	Italy	C. Baitone–V. del Miller Parco Adamello Tredenus–Frisozzo	Dupré et al. (2001), Apollonio et al. (2009)
G21	Italy	Alto Garda–Tombea–Caplone	Dupré et al. (2001), Apollonio et al. (2009)
G22	Italy	Palla Bianca–Weisskugel Tessa–Senales Tribulaun	Dupré et al. (2001), Apollonio et al. (2009)
G23	Italy	Cima Dura–Durreck Ponte di Ghiaccio–Eisbruggspitze Tauri–Tauern Val di Vizze–Pfitschertal	Dupré et al. (2001), Apollonio et al. (2009)
G24	Italy	Antelao–Marmarole Croda Rossa–Croda del Becco Monzoni–Marmolada Pale di S. Martino Sella	Dupré et al. (2001), Apollonio et al. (2009)
G25	Italy	Dolomiti Friulane	Apollonio et al. (2009)
G26	Italy	Monte Canin Monte Plauris Tarvisio	Apollonio et al. (2009)

Analysis of paired–data from summer and winter counts (*n* = 24) suggested that Alpine ibex abundance in summer counts is underestimated when compared to winter counts (mean absolute difference = –15 ± 14 ibex; mean relative difference = –22 ± 13%; paired *t*–test: $t = -2.22$, $P < 0.05$, df = 23).

Using only the count data from countries with Alpine ibex populations (Italy, Switzerland, France, Austria, Germany, Slovenia), our GAM model predicted (estimate ± se) an overall population of 49,037 ± 1,012 individuals in 2013. Predicted values using only count data were also estimated for the three main countries with Alpine ibex (Italy, Switzerland and France; table 4, fig. 2). Data compiled for the other countries include several count estimations, but no long–term series that would have allowed us to build accurate and comparable models at a national scale for Austria, Germany and Slovenia. Nevertheless, in table 4 we summarize the population estimates reported in previous studies. Using CMR data when available and count data if not available, our GAM model predicted an overall population of 50,195 ± 1,012 individuals in 2013 (see table 4 for national predictions).

Estimated distribution

Using the available data on spatial distribution from the main countries harbouring Alpine ibex populations (Italy, Switzerland and France), our GAM model predicted (estimate ± se) a distribution of 5,058 ± 109 km² in

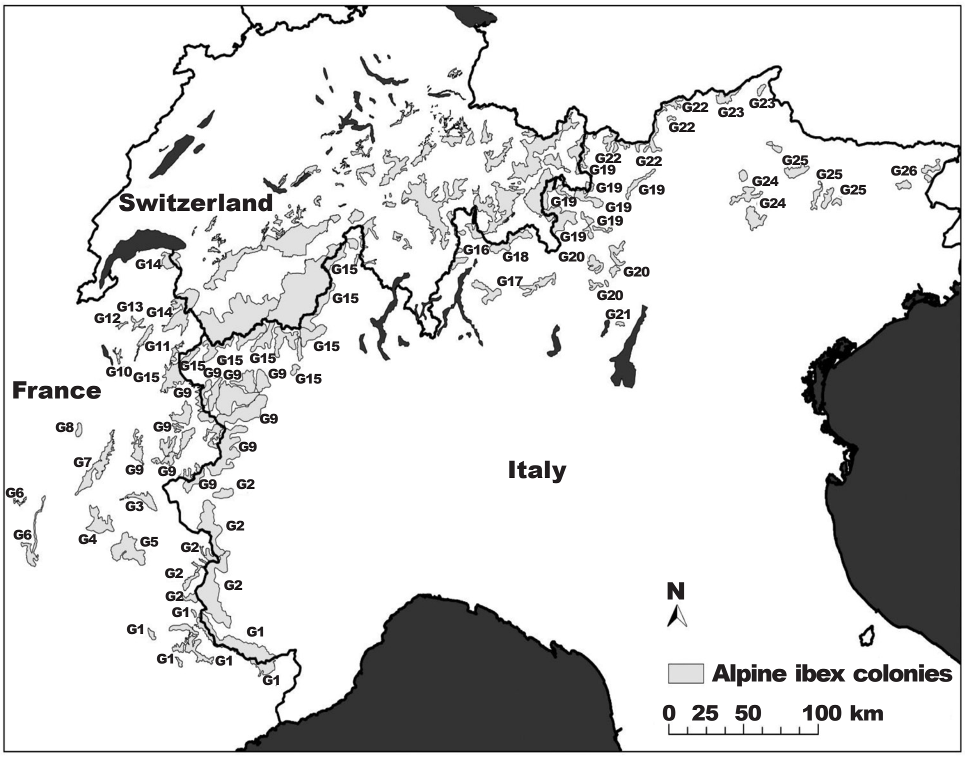

Fig. 1. Distribution of the Alpine ibex colonies, *Capra ibex*. Lakes and the sea are depicted in dark grey, black lines are national boundaries. Redrawn from Apollonio et al. (2009), Corti (2012) and Office fédéral de l'environnement (2013a). See table 2 for the identity of the meta–populations.

Fig. 1. Distribución de las colonias del íbice de los Alpes, Capra ibex*. El mar y los lagos se muestran en gris oscuro, las fronteras de los países son las líneas negras. Adaptado de Apollonio et al. (2009), Corti (2012) y Office fédéral de l'environnement (2013a). Véase la tabla 2 para consultar la identidad de las metapoblaciones.*

Italy and 2,568 ± 88 km² in France (table 4, fig. 3) for 2013. Data compiled for other countries (Switzerland, Austria, Germany and Slovenia) were too limited to be able to build reliable models or to predict estimated distributions for the whole range of the Alpine ibex.

Disease outbreaks

Several disease outbreaks associated with population decreases between 1975 and 2013 have been reported in the literature (table 2). The best model of the factors associated with the start of disease outbreak (AIC weight = 0.16) included only the factor 'density' (table 5, fig. 4A). Five other models were within 2 AIC units of the best model, all of which included the factor 'density' within other factors (year, abundance and country). The deviance explained by these six models ranges from 15.6% to 19.2% (table 5). The relative importance of variables underlined once more the fact that, of the tested variables, local density was the key factor associated with the appearance of a disease outbreak, although local abundance, year and country might also play role (table 5).

The best model for the persistence of disease outbreak (AIC weight = 0.41) included four parameters: density, local abundance, year and meta–population. Two other models were within 2 AIC units of the best model and include (in addition to the previous four parameters) 'monitoring season' or 'country'. The deviance explained by these best models was about 70% (table 6, fig. 4B–4D).

Discussion

Abundance and distribution

The predicted values of the GAMs suggest that, in agreement with national reports, at both national and international scales, the Alpine ibex has increased in abundance (fig. 2) (Apollonio et al., 2009; Corti, 2012). Only the three countries with the largest ibex populations (Italy, Switzerland and France) have information from long–term monitoring schemes and up–to–date data from Austria, Germany and Slovenia would improve the overall estimates of ibex abundance in Europe. Analyses of paired data show that methodological designs have a major impact on the

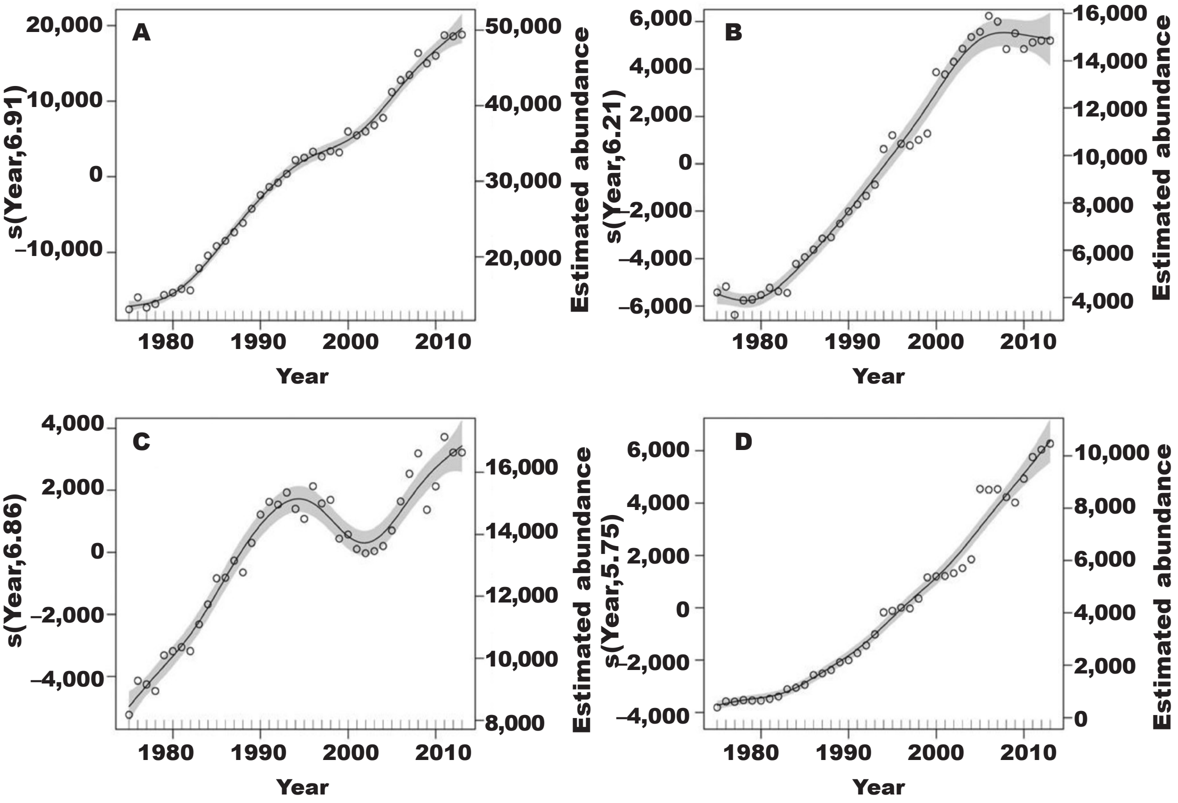

Fig. 2. Evolution of the abundance of the Alpine ibex, *Capra ibex*, between 1975 and 2013 in the whole of the Alps (A), Italy (B), Switzerland (C) and France (D). The solid lines represent the predicted patterns estimated by the generalized additive models, the grey shaded areas indicate the standard error, and the open circles are the observed values. The left–hand *y*–axis represents the centred values and specifies the smoothing factor 'Year', with the approximate degrees of freedom. The right–hand *y*–axis represents the estimated ibex abundance.

Fig. 2. Evolución de la abundancia del íbice de los Alpes, Capra ibex*, entre los años 1975 y 2013 en toda la cordillera de los Alpes (A), Italia (B), Suiza (C) y Francia (D). Las líneas continuas representan los patrones estimados por los modelos aditivos generalizados, las zonas sombreadas en gris indican el error estándar y los círculos son los valores observados. El eje de las Y de la izquierda representa los valores centrados y especifica el parámetro suavizado "Año", con los grados de libertad aproximados. El eje de las Y de la derecha representa la abundancia estimada de íbices.*

estimates of population abundance: abundances are underestimated in summer vs. winter counts and in census counts *vs.* CMR estimates. Although count data is the main source of population information in the literature, judging from our sample, on average they underestimate by half the Alpine ibex abundance when compared with results from CMR. Thus, most available information on ibex abundance (including the estimates in table 4) should be handled with care and is best thought of as an indicator of relative abundance rather than an accurate estimate of population size. The biases observed suggest that the Alpine ibex is probably more abundant that usually reported. Our total population estimate for Alpine ibex (about 50,200 individuals) is derived essentially from counts, while the total estimate for the Iberian ibex *Capra pyrenaica* population (about 50,000 individuals according to Pérez et al. (2002)) are largely derived from line transects and distance sampling. Our results show that the mean bias of Alpine ibex counts leads to underestimations. However, the mean bias of Iberian ibex estimates —as for other mountain ungulates—is an issue that is still unresolved because the use of data truncation in distance sampling analysis can overestimate densities of mountain ungulates, and consequently, their abundance (Pérez et al., 2015). Thus, Alpine ibex may well be the most abundant ibex in Western Europe. Further studies will be required to refine monitoring methods and population estimates of mountain ungulate species.

Table 4. Abundance and distribution of Alpine ibex *Capra ibex* in 2013: Scd. Sum of count data only; P–GAM. Predicted by a GAM (generalized additive model) of count data; S–CMR. Sum of count plus CMR data when available; P–GAM–CMR. Predicted by a GAM of count data plus CMR data when available; Srp. Sum of reported population ranges; P–GAMrd. Predicted by a GAM of reported range data; * Reported from previous estimates; – Insufficient data available.

Tabla 4. Abundancia y distribución del íbice de los Alpes, Capra ibex*, en 2013: Scd. Suma de los datos obtenidos únicamente mediante censo; P–GAM. Estimación mediante un GAM (modelo aditivo generalizado) de los datos de censo; S–CMR. Suma de los datos de censos más los obtenidos con métodos de captura, marcaje y recaptura, si se dispone de ellos; P–GAM–CMR. Estimación mediante un GAM de los datos de censos más los obtenidos con métodos de captura, marcaje y recaptura, si se dispone de ellos; Srp. Suma de las áreas de distribución de la población registradas; P–GAMrd. Estimación mediante un GAM de los datos relativos a las áreas de distribución registradas; * Registrado en estimaciones anteriores; – Datos disponibles insuficientes.*

	Population size				Distribution range	
Country	Scd (ibex)	P–GAM (ibex ± se)	S–CMR (ibex)	P–GAM–CMR (individuals ± se)	Srp (km²)	P–GAMrd (km² ± se)
Italy	14,854	14,884 ± 588	14,854	14,879 ± 590	4,753	5,058 ± 109
France	9,302	9,819 ± 454	10,475	10,549 ± 453	2,509	2,568 ± 88
Switzerland	16,645	16,839 ± 436	16,645	–	–	–
Austria*	6,730*	–	6,730*	–	–	–
Germany*	400*	–	400*	–	–	–
Slovenia*	300*	–	300*	–	–	–
Total	48,231	49,037 ± 1,012	49,404	50,195 ± 1,012	–	–

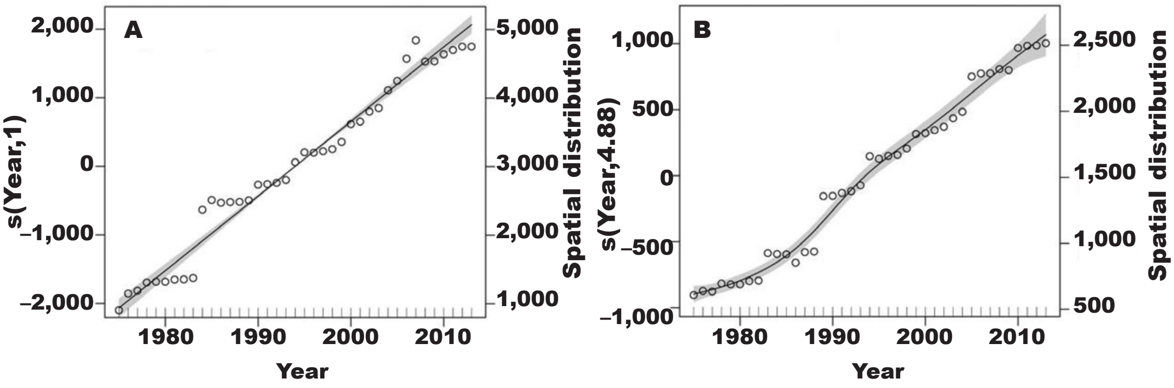

Fig. 3. Evolution of the spatial distribution of the Alpine ibex, *Capra ibex*, between 1975 and 2013 in Italy (A) and France (B). The solid lines represent the predicted patterns estimated by the generalized additive models, the grey shaded areas indicate the standard error, and the open circles are the observed values. The left–hand *y*–axis represents the centred values and specifies the smoothing factor 'Year', with the approximate degrees of freedom. The right–hand *y*–axis represents the estimated spatial distribution of ibex (km²).

Fig. 3. Evolución de la distribución espacial del íbice de los Alpes, Capra ibex*, entre los años 1975 y 2013 en Italia (A) y Francia (B). Las líneas continuas representan los patrones estimados por los modelos aditivos generalizados, las zonas sombreadas en gris indican el error estándar y los círculos son los valores observados. El eje de las Y de la izquierda representa los valores centrados y especifica el parámetro suavizado "Año", con los grados de libertad aproximados. El eje de las Y de la derecha representa la distribución espacial estimada de íbices (km^2).*

Table 5. Model selection for factors associated with the appearance of disease outbreaks in Alpine ibex *Capra ibex* at population scale in Italy and France. D. Density; A. Abundance; Y. Year; G. meta–population; C. Country; S. Season of counts; P. population; *n*. Sample size; *K*. Number of estimated parameters; AIC. Akaike's information criterion; ∆AIC. Difference of AIC between the model and the most–parsimonious model; 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 following Burnham & Anderson (2002) and Wood (2006).

Tabla 5. Selección de modelos para determinar los factores asociados con la aparición de brotes de enfermedades en el íbice de los Alpes, Capra ibex*, a escala poblacional en Francia e Italia. D. Densidad; A. Abundancia; Y. Año; G. Metapoblación; C. País; S. Estación de los censos; P. Población;* n. *Tamaño muestral;* K. *Número de parámetros estimados; AIC. Criterio de información de Akaike; ∆AIC. Diferencia del AIC entre el modelo y el modelo de máxima parsimonia; L(gi/x). Probabilidad de que el modelo sea el mejor dado el conjunto de datos; Wi. Peso de Akaike del modelo; Dev–expl. Desviación explicada del modelo ajustado; RI. Importancia relativa de los factores. Solo se muestran los diez modelos mejores según Burnham & Anderson (2002) y Wood (2006).*

Model	*n*	*K*	AIC	∆AIC	L(gi/x)	Wi	Dev–expl	RI	
D	704	3	153.22	0.00	1.00	0.16	15.60	D	1.00
D+Y	704	5	153.67	0.44	0.80	0.13	18.20	Y	0.54
D+A	686	3	153.99	0.77	0.68	0.11	15.20	A	0.50
D+A+Y	686	5	154.14	0.92	0.63	0.10	17.70	C	0.34
D+Y+C	704	6	154.24	1.01	0.60	0.10	19.20	S	0.28
D+A+Y+C	686	6	155.01	1.78	0.41	0.07	19.10	G	0.00
D+A+C	686	5	155.33	2.10	0.35	0.06	15.90	P	0.00
D+A+Y+C+S	686	11	155.54	2.32	0.31	0.05	25.60		
D+S	704	5	155.60	2.38	0.30	0.05	17.00		
D+A+C+S	686	9	155.91	2.69	0.26	0.04	22.30		

In agreement with the predictions of ibex dynamics, information on the distribution of the Alpine ibex suggests that overall increases in ibex populations have occurred in Italy and France (fig. 3). The structure of the observed values (figs. 2–3) suggests that information on distribution has been updated less often than abundance estimates. Thus, further studies — particularly in ibex populations in Switzerland, Austria, Germany and Slovenia— would improve the present understanding of ibex distribution across Europe.

Abundance and distribution data, taken together, suggest that the IUCN 'Least Concern' conservation status is probably accurate at an international scale and at a national scale for Italy, Switzerland and France.

Population units

Analyses of epidemiological *vs.* demographic data show that the population units used for historical or practical reasons by institutions to monitor and manage ibex populations are excluded from the best models. However, the proxy for meta–populations that take into account the reported connections between populations is selected in the best models. Thus, the spatial structure and connectivity of ibex colonies must also be taken into account. These results also underline the relevance of trans–boundary monitoring and management, such as the programmes already underway in the Vanoise (France), Gran Paradiso (Italy) (Girard et al., 2009) and Mercantour (France) National Parks, and the Alpi Maritime Natural Park (Italy) (Parc National Le Mercantour & Parco Naturale Alpi Marittime, 2006).

Disease outbreaks

In agreement with theoretical models (Anderson & May, 1979; Lloyd–Smith et al., 2005), our results highlight the link between the local density of Alpine ibex and appearance and persistence of disease outbreaks (fig. 4), a finding that agrees with the results of recent studies of pneumonia epizootics in bighorn sheep (Sells et al., 2015). Moreover, ibex abundance and year were associated with at least the persistence of disease outbreaks (fig. 4C–4D). For the start of outbreaks, the deviance explained by the best models (15.6–19.2%) suggests that most of the variability in the appearance of disease outbreaks for

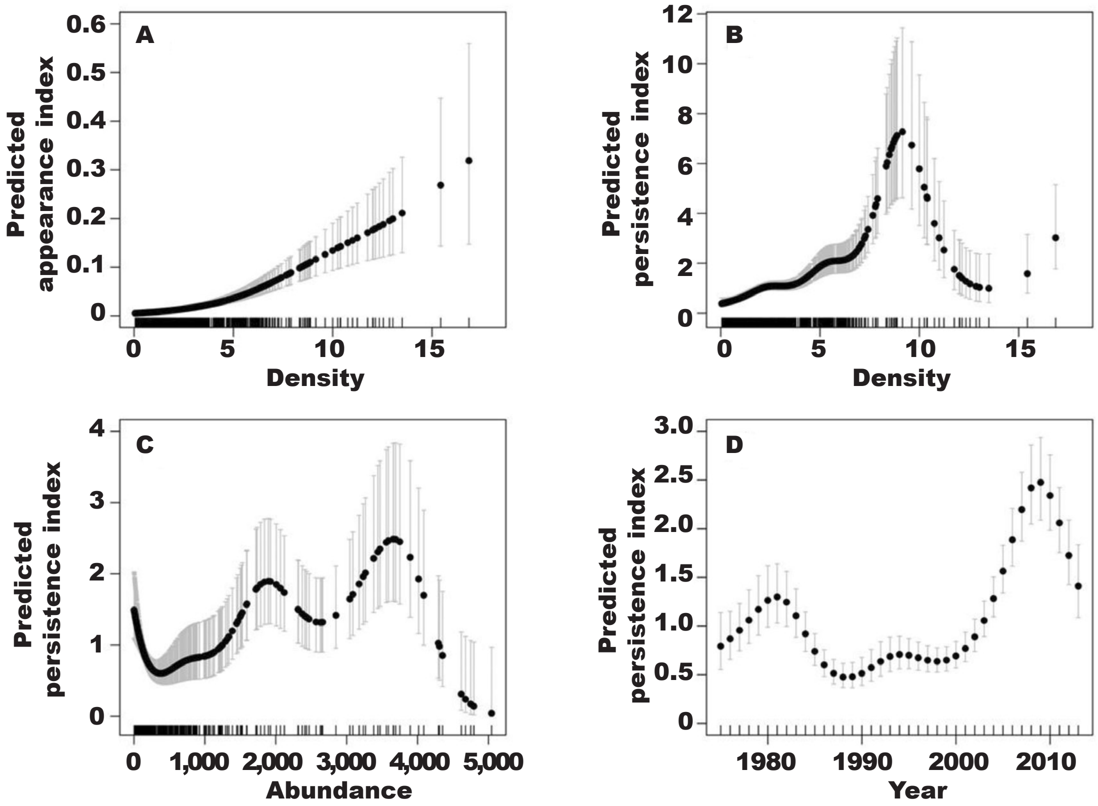

Fig. 4. Link between the appearance and the persistence of disease outbreaks in the Alpine ibex, *Capra ibex*, and density estimates (A, B), abundance (C) and year (D). The solid circles represent the predicted values estimated by the best generalized additive models for the available data, the grey bars indicate the standard error, and the thick lines represent the values with available observed data. The left–hand *y*–axis represents the relative probability of a disease outbreak (A) and the relative persistence of disease outbreaks (B, C, D).

Fig. 4. Relación entre la aparición y la persistencia de brotes de enfermedades en el íbice de los Alpes, Capra ibex*, y las estimaciones de densidad (A, B), la abundancia (C) y el año (D). Los puntos representan los valores previstos estimados con los mejores modelos aditivos generalizados para los datos disponibles, las líneas grises indican el error estándar y las líneas gruesas representan los valores con los datos observados disponibles. El eje de las Y de la izquierda representa la probabilidad relativa de que se produzca un brote de enfermedad (A) y la persistencia relativa de los brotes de enfermedades (B, C, D).*

the available data is not explained by local density and the other parameters included in our analyses. Thus, exposure to pathogens (encounter filter), defined as the probability of contact between the pathogen and the potential host population (Combes, 2001), rather than compatibility (compatibility filter), defined as the population predisposition as suitable environments for potential outbreaks, might be key to the appearance of disease outbreaks. In terms of outbreak persistence, the deviance explained by the best models was about 70%, which suggests that the considered factors of population compatibility to outbreaks explain most of the observed variability in the persistence of disease outbreaks. Thus, our results match the hypothesis of density–dependence for pathogen transmission and highlight the idea that disease outbreaks may persist longer in high–density populations, at least in the areas with the commonest high–density values (7–10 ibex/km²). Nevertheless, our results also reveal a decrease in the persistence index at greatest density and abundance values (density greater than 10 ibex/km² and abundance over 4,000 individuals in the population), probably due to the low sample size for this range of values and the poorer accuracy of demographic and epidemiological data in the largest populations. The non–linear pattern linking the persistence of outbreaks and ibex abundance also suggests a localized decreasing pattern for small populations (0–350 ibex in the population). This pattern might be a localized artefact for this range of values due to the early intensive monitoring of reintroduced populations. However, it could also indicate an 'Allee

Table 6. Model selection for factors associated with persistence of disease outbreaks in Alpine ibex *Capra ibex* at population scale in Italy and France. D. Density; A. Abundance; Y. Year; G. meta–population; S. Season of counts; C. Country; P. population; *n*. Sample size; *K*. Number of estimated parameters; AIC. Akaike's information criterion; ∆AIC. Difference of AIC between the model and the most–parsimonious model; 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 following Burnham & Anderson (2002) and Wood (2006).

Tabla 6. Selección de modelos para determinar los factores asociados con la persistencia de brotes de enfermedades en el íbice de los Alpes, Capra ibex*, a escala poblacional en Francia e Italia. D. Densidad; A. Abundancia; Y. Año; G. Metapoblación; S. Estación de los censos; C. País; P. Población;* n*. Tamaño muestral;* K*. Número de parámetros estimados; AIC. Criterio de información de Akaike; ∆AIC. Diferencia del AIC entre el modelo y el modelo de máxima parsimonia; L(gi/x). Probabilidad de que el modelo sea el mejor dado el conjunto de datos; Wi. Peso de Akaike del modelo; Dev–expl. Desviación explicada del modelo ajustado; RI. Importancia relativa de los factores. Solo se muestran los diez modelos mejores según Burnham & Anderson (2002) y Wood (2006).*

Model	*n*	*K*	AIC	∆AIC	L(gi/x)	Wi	Dev–expl	RI	
D+A+Y+G	686	49	306.97	0.00	1.00	0.41	70.12	D	1.00
D+A+Y+G+S	686	49	308.09	1.11	0.57	0.24	69.86	A	1.00
D+A+Y+G+C	686	49	308.13	1.16	0.56	0.23	70.20	Y	1.00
D+A+Y+G+C+S	686	50	309.45	2.47	0.29	0.12	69.99	G	1.00
A+Y+G+S	688	36	327.45	20.48	0.00	0.00	58.61	S	0.36
A+Y+G	688	34	328.17	21.19	0.00	0.00	57.82	C	0.35
D+A+Y+C+S	686	21	329.51	22.53	0.00	0.00	50.68	P	0.00
D+A+Y+S	686	21	336.17	29.19	0.00	0.00	49.04		
D+A+Y+C	686	22	337.96	30.99	0.00	0.00	48.96		
D+Y+G	704	40	338.01	31.04	0.00	0.00	58.49		

effect' linked to pathogens (Krkošek et al., 2013). The persistence index of outbreaks was greatest in very small and in large populations, that is, populations that are possibly at the edge and the core, respectively, of the ibex's range. Increased persistence in very small populations (edge of range) might be the result of repeated exposure or greater compatibility of colonies to pathogens, of contact or competition with livestock (Sells et al., 2015), or of high gregariousness in very small populations. Increased persistence in large populations (core of range) might be linked to areas with the high density of potential hosts that usually characterizes large populations. The observed links between outbreaks and density were non–linear and the patterns suggest relative threshold values (Lloyd–Smith et al., 2005) close to five and seven, respectively, for the appearance and persistence of disease outbreaks. As discussed in previous articles on wild species (Gortazar et al., 2006; Cross et al., 2010), environments favouring overabundant and aggregated populations (*e.g.,* protected areas in the case of the Alpine ibex) sometimes also leave populations more prone to persistent disease outbreaks. Many threatened populations, species and rich ecosystems throughout the world are now protected. A new conservation challenge is emerging because protected populations on the increase may suffer from repeated disease outbreaks due to over–abundance facilitated by protection (Gortazar et al., 2006; Cross et al., 2010). Further studies will have to explore these conservation trade–offs (Leader–Williams et al., 2010) to ensure that management plans that are designed in one particular year but are then implemented year–after–year do not evolve into conservation threats.

Additionally, our results suggest that disease rose in the Alpine ibex in 2000–2010 despite its decrease in the 1980s. This decrease in the 1980s was probably the result of technical advances in diagnosis and increased investment in livestock prophylaxis (*e.g.,* Fensterbank, 1986), coupled with research in eco–pathology and the management of disease risk at the wildlife–livestock interface during this period (*e.g.,* Mayer et al., 1996). Nevertheless, the positive trends in Alpine ibex populations and the observed association between the demographic rise of ibex and disease outbreaks suggest that compatibility to epizooties may be increasing —or may already be high— in several populations of *Capra ibex*.

Proposal for further studies

The heterogeneity of Alpine ibex monitoring between populations prevented us from inferring abundance or distribution estimates for Switzerland, Austria, Germany or Slovenia. Further investment aimed at updating missing information would thus complete the data presently available for Alpine ibex.

Potential double counts in trans–boundary populations might also have affected abundance estimates. Nevertheless, the observed propensity to undercount probably compensates for double counts and further trans–boundary monitoring will probably minimize this potential bias.

Population structures are still too poorly documented, however, to be incorporated into our analyses (even though they may modulate demographic processes) (Yoccoz & Gaillard, 2006; Mignatti et al., 2012). Thus, further studies should explore the role of population structure as a potential modulating factor of population compatibility to disease outbreaks.

Outbreaks are relatively rare events and the available data do not allow for each disease to be analysed separately. In light of fresh outbreaks in the future, analysis should continue in the future, as should the search for potential variability in threshold values between pathogenic agents. Even so, our analysis permits us to explore factors that may determine associations with disease outbreaks at population scales.

In conclusion, our reappraisal of the available demographic and epidemiologic data on Alpine ibex highlights the methodological limitations, the increase in ibex populations, the increased risk of disease outbreaks and the links between host demography and disease outbreaks. A challenge for the future is how to integrate knowledge on density–dependent processes in wild species (*e.g.* disease outbreaks in the Alpine ibex) into the management of such species and ecosystems.

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