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REVIEW

The successful introduction of the alpine marmot *Marmota marmota* in the Pyrenees, Iberian Peninsula, Western Europe

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ABSTRACT

1. The introduction of non-native species can pose environmental and economic risks, but under some conditions, introductions can serve conservation or recreational objectives. To minimize risks, introductions should be conducted following the International Union for Conservation of Nature's guidelines and should include an initial assessment and a follow-up.

2. In 1948, to reduce the predation pressure on Pyrenean chamois *Rupicapra pyrenaica pyrenaica* by golden eagles *Aquila chrysaetos*, the alpine marmot *Marmota marmota* was introduced to the Pyrenees in Western Europe. In successive introductions, about 500 marmots were released, but the fate of the released animals and their impacts on the environment remain largely unstudied.

3. The aim of this study was to assess the success of the introduction of the alpine marmot into the Pyrenees, 60 years after the initial release, and the potential impacts of this species on Pyrenean ecosystems.

4. We reviewed what is known about the marmot populations introduced to the Pyrenees and other populations within their native range in the Alps, particularly in

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terms of population structure and dynamics, habitat use and potential environmental impacts.

5. The alpine marmot is widely distributed and, apparently, well established in the Pyrenees. Population structure and demographic parameters are similar within and outside the historical distribution range of the species, and habitat suitability is one of the main reasons for the species' success in the Pyrenees. Few researchers have investigated the impacts of alpine marmots in the Pyrenees; thus, those impacts have to be inferred from those observed in the species' native range or in other species of marmot. Introduced alpine marmots are likely to impact on Pyrenean grasslands through grazing and burrowing, have the potential to alter Pyrenean food webs and could act as vectors of parasites and disease.

6. Although the introduction of the alpine marmot in the Pyrenees appears to have been successful, more needs to be known about the effects of the established populations on the environment before informed management actions can be taken in the Pyrenees.

Keywords: alien species, biogeographical comparison, herbivore, mountain ecosystems, translocation

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INTRODUCTION

The intentional release of living organisms into the wild, the so-called translocation, can be carried out in order to achieve species conservation goals (Griffith et al. 1989). The International Union for Conservation of Nature (IUCN) recognizes three main types of translocation: introduction, reintroduction and restocking (Anonymous 1987). Introductions involve the dispersal by human agency of a living organism outside its historical distribution range, while reintroductions involve the release of a species into the native range from which it disappeared in historical times (Anonymous 1998). Restocking is a means of increasing the size of a population. While reintroductions typically have been viewed as valid means of conserving species (e.g. Halley 2011), introductions of non-native species have often had harmful effects on native species, ecosystems and human well-being. Non-native species, especially if they become invasive, can have negative effects on the dynamics of natural systems, which can lead to the extirpation of native species and significant economic losses (Anonymous 2000). Biological invasions are an increasing threat to biodiversity (Soorae 2010), and generally, the IUCN discourages species introductions (Anonymous 1987).

Some introductions, however, can be beneficial to humans or natural communities, e.g. by providing sources of food or habitat for rare or declining species, by acting as functional substitutes for extinct species or by providing desirable ecosystem functions (Schlaepfer et al. 2011). Thus, in some circumstances, the introduction of a species into an area that is outside its historical native range can be a valid conservation tool (Thomas 2011). In any case, to avoid unnecessary risks, introductions should comply with the IUCN guidelines and should include an initial assessment phase and monitoring of released animals after the introduction (Anonymous 1987). Ideally, the potential effects of the introduced species on ecosystem functioning should be assessed. However, in many instances, introductions have not been followed up.

The alpine marmot *Marmota marmota* was introduced to the Pyrenees, a region that is outside of the historical distribution range of the species, first by individual hunters (Couturier 1955) and then by the staff of the Parc National des Pyrénées, France, with the objectives of reducing the predation pressure on Pyrenean chamois *Rupicapra pyrenaica pyrenaica* by golden eagles *Aquila chrysaetos* and providing food for brown bears *Ursus arctos* (Besson 1971). Unfortunately, the results and effects of the introduction and the achievement of its goals remain largely untested. From the release points in southern France, the species spread rapidly into the southern Pyrenees, probably because the habitats were favourable, and because natural predators and important interspecific competitors were absent (Herrero et al. 1987, 1992). Alpine marmots seem to be well established in the Pyrenees, but the status of the populations is uncertain.

A translocation is successful if it produces a self-sustaining population (Griffith et al. 1989, Williamson & Fitter 1996); however, to understand fully the success of an introduction, the ecology of populations within and outside the species' native range has to be compared (Hierro et al. 2005). Such comparative studies can help in the assessment of the impact of non-native species within their introduced range (Hufbauer & Torchin 2007). Introduced mammals can have an impact on the environment through, e.g. herbivory, the transmission of diseases or other effects on agriculture, livestock and forestry. Furthermore, the effects are likely to be greater in the areas occupied by the introduced populations than they are in the areas of the species' native distribution (Kumschick et al. 2011).

In this study, we review what is known about the alpine marmot populations that became established after introductions in the Pyrenees. In addition, we describe the past and present distribution of alpine marmots and compare the populations of alpine marmot in the Pyrenees with those within the species' native range, comparing habitat selection, population parameters and life-history traits reported in the literature. We examine the potential effects of alpine marmots on ecosystems in the Pyrenees. We propose hypotheses for the possible fate of their populations under global change scenarios, based on available information from the native range of the species and from other marmot species.

METHODS

To assess the status of alpine marmot populations within the species' native range and those that were introduced to the Pyrenees, we searched the published and unpublished literature for information on specific aspects of the species' ecology, following the guidelines proposed by Pullin and Stewart (2006). Specifically, between January and April 2011, we searched electronic databases (Scholar Google, ISI Web of Knowledge, Scopus, ScienceDirect), professional networks (International Marmot Network) and bibliographies, and consulted experts. We focused on key aspects of the population structure and dynamics of alpine marmots and their potential impacts on Pyrenean ecosystems. The searches were based on the following terms: alpine marmot, *Marmota*, Pyrenees, introduction, habitat, population, dynamics, impact, diet, vegetation, predator, soil and burrow. Sources of information covered from 1845 to date (2011). 1

When authors reported quantitative data for native and introduced populations (Table 1), we used a *Z*-test to compare the average values of each type of population, weighted by the variances of each study. When studies were suspected to be non-independent (i.e. when different studies included data from the same marmot populations or from a subset of populations), analyses were repeated with and without those studies; in all cases, results were consistent, so we report here results of analyses pooling all studies. Analyses were performed using R 2.10.1 (Anonymous 2009).

RESULTS

Past and present distributions of alpine marmots

The alpine marmot was widely distributed in Europe during the Quaternary, but after the last glaciation, it became restricted to the Alps (Western Europe) and Tatra Mountains (Central Europe), because increases in temperatures promoted the expansion of forests which forced marmots to move to higher elevations (Zimina & Gerasimov 1973). In addition, human activities have had a strong influence on the present distribution of alpine marmots. The human consumption of marmots and over-hunting led to successive extinctions of local populations within their historical range (Preleuthner 1999), while translocations have increased the species' distribution (Ramousse et al. 1993). As well as to the Pyrenees, alpine marmots were introduced to the Apennines (Italy), the Carpathians (Central and Eastern Europe) and the Eastern Alps outside their native distribution range (Preleuthner et al. 1995), and were reintroduced to several areas in the Alps (Ramousse & Le Berre 1993b).

Fossils of alpine marmots from the late Pleistocene have been found in the Pyrenees (Villalta 1972), but Pyrenean populations presumably disappeared after the last glaciations. Although there are historical references to the species in the region (e.g. Comte 1845, Vilanova 1872), authors appear to have repeated erroneous information, and the widely accepted view is that alpine marmots were not in the Pyrenees in historical times (Astre 1946, Herrero et al. 2002).

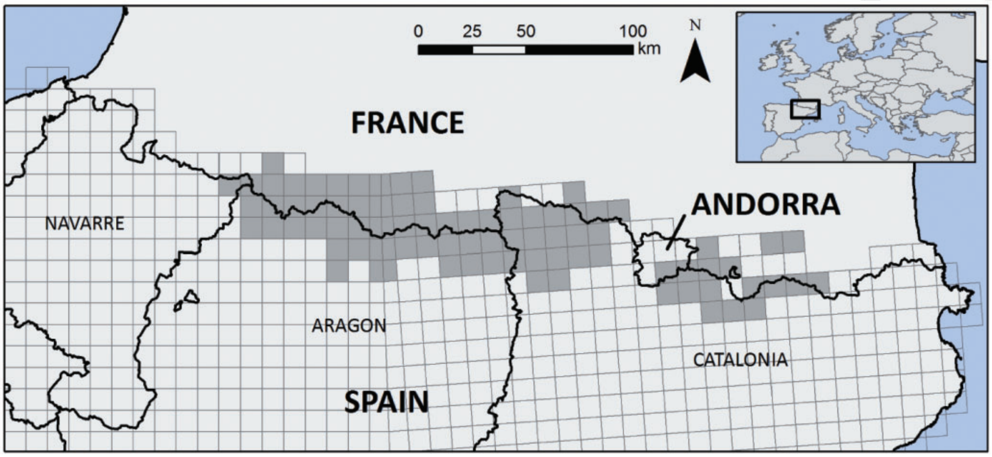
Efforts to establish populations of alpine marmots in the Pyrenees began in France in 1948 (Couturier 1955), were intensified in the 1960s and 1970s (Ramousse et al. 1993) and continued until 1988 (Ramousse et al. 1992). Quickly, stable populations formed in the French Pyrenees and, from there, marmots dispersed southward and established populations in the southern Pyrenees (Herrero et al. 1987). Throughout much of the southern Pyrenees, the expansion of alpine marmot populations has been rapid (Canut et al. 1989, Herrero et al. 1992, González-Prat et al. 2001, Giboulet et al. 2002). Rapid expansion defines invasive species (i.e. species with high invasion rates which occupy suitable habitat rapidly; López et al. 2009a, b). Today (2011), alpine marmots occur in most areas of the southern Pyrenees, and previous estimates suggest that the species occupies c. 8200km^2 (Fig. 1), but this information needs to be updated. Contemporary information on the distribution of the species is available for populations in Spain and Andorra, but not for those in France.

Globally, the alpine marmot is classified as a species of Least Concern by the IUCN (Herrero et al. 2008). Its legal status varies throughout its native range and in the Pyrenees. In France, the alpine marmot is a game species, but in Andorra, it is a protected species. In Spain, the species is categorized as introduced in Navarre, of special interest in Aragon, and as a game species which is not allowed to be hunted in Catalonia (Herrero et al. 2002).

Table 1. Structure of alpine marmot populations in their native range (the western Alps) and in the Pyrenees: average family group size (number of individuals), mean number of young per family group, home range size of the family group (ha) and density estimates (marmots ha^{-1})

	Sample size (duration of study, years)	Family group size	Young/family	Home range size (ha)	Density (individuals ha^{-1})	Reference
Native range						
French Alps (La Vanoise NP)	50 (1)	5.52 ± 0.21	1.36 ± 0.04	2.50 ± 0.07	–	Allainé et al. (1994)
French Alps (La Vanoise NP)	4 (1)	7.31 ± 2.44	2.25 ± 2.06	2.18 ± 0.87	3	Perrin et al. (1993)
French Alps (La Vanoise NP)	4 (1)	9.00 ± 2.45	3.00 ± 0.82	–	–	Barash (1976)
French Alps (La Vanoise NP)	3 (1)	6.33 ± 3.79	–	–	–	Perrin et al. (1992)
French Alps (La Vanoise NP)	11 (1)	4.45 ± 2.98	–	–	–	Giboulet (1997)
French Alps (Hautes Alpes)	4 (4)	11.00 ± 4.44	2.58 ± 0.78	1.26 ± 0.26	1.18	Mann and Janeau (1988)
German Alps (Berchtesgaden NP)	21 (13)	–	3.47 ± 1.47	–	–	Stephens et al. (2002)
Italian Alps (Gran Paradiso NP)	3 (7)	7.20 ± 4.11	–	1.83 ± 0.43	–	Lenti Boero 2003)
Italian Alps (Gran Paradiso NP)	27 (10)	4.71 ± 2.90	–	–	1.03	Lenti Boero 1999)
Italian Alps (Gran Paradiso NP)	–	–	–	–	0.36	Peracino and Bassano (1992)
Swiss Alps	12 (2)	7.75 ± 2.70	–	1.58 ± 0.23	–	Zelenka (1965)
		6.09 ± 0.14	**1.56 ± 0.04**	**2.08 ± 0.04**	**1.39 ± 1.13**	
Pyrenees						
Andorra	– (1)	4.87 ± 2.96	–	–	1.40	Riba and Tena (1999)
Navarre (Larra-Belagoa NR)	10 (1)	5.30 ± 2.58	2.60 ± 0.50	–	–	Herrero et al. (1996)
Navarre (Larra-Belagoa NR)	2 (1)	–	–	0.79 ± 0.16	0.77	Herrero and García-Serrano (1994)
Aragon (Ordesa and Monte Perdido NP)	11 (1)	4.00 ± 2.24	1.82 ± 1.54	–	0.59	García-González et al. (2003)
Aragon (Piedrafita valley)	14 (2)	5.20 ± 0.62	2.71 ± 2.02	–	0.66	Herrero et al. (1999)
French Pyrenees (PN des Pyrénées)	4 (2)	6.50 ± 2.00	3.00 ± 1.05	–	–	Nogué and Arthur (1992)
French Pyrenees (PN des Pyrénées)	–	–	–	–	1.74	Salharang (2001)
French Pyrenees (Nohèdes NR, Pyréenées Orientales)	2 (1)	–	–	–	1.10	Cayatte (1997)
French Pyrenees (Massif du Madres-Coronat)	7 (1)	4.57 ± 2.64	–	–	–	da Ros and Chazel (1997)
		5.15 ± 0.27	**2.58 ± 2.40**	**0.79 ± 0.16**	**0.90 ± 0.34**	

NP, National Park; NR, Nature Reserve; –, no data available.
Mean ± standard deviations are shown. Sample sizes (number of family groups) and length of each study (years, in parentheses) are indicated and were used to calculate all population parameters except density. Density (marmots ha^{-1}) was estimated by multiplying the average number of marmots per territory (i.e. family size) by the number of burrows in suitable habitats in each study area. Weighted means for each area (±standard deviation) are given in bold (see text for details), except for density, where arithmetic means (±standard deviation) are shown.



Colour

Fig. 1. Reported distribution of alpine marmot in the Pyrenees (10 × 10 km Universal Transverse Mercator grid). Dark grey shaded cells have marmots. Data are from Herrero & García-González (2007; southern Pyrenees, Spain), Jean (1979) and expert opinion because no current distribution of marmots is available (France), and from expert opinion only (Andorra). 11

Habitat selection and use by marmots in introduced populations in the Pyrenees

A sufficiently large founder population and the presence of suitable habitats are vital to the success of the translocations of alpine marmots (Neet 1992, Ramousse & Le Berre 1993b). Estimates suggest that more than 500 marmots from La Vanoise and Mercantour National Parks in the French Alps were released, successively, in the French Pyrenees (Ramousse et al. 1992). Marmot populations in the Pyrenees have high genetic variability and are still closely related to the autochthonous populations in the French Alps (Kruckenhauser et al. 1999).

Alpine marmots occupy alpine, subalpine and high montane grasslands throughout Western Europe (Mann et al. 1993). Suitable habitats include open grassland areas above or near the treeline, rocky areas, moderate to steep slopes that provide good drainage, friable soils that can support burrows and eastern to southern exposures where snow melts earlier (Armitage 2000). In the Alps, alpine marmots prefer areas that have a southern exposure, moderate slope and moderate plant cover (Rodrigue et al. 1992, Allainé et al. 1994).

Generally, alpine marmots occupy habitats in the Pyrenees that are similar to those occupied in the Alps (Herrero et al. 1994a, Herrero & García-González 2007, López et al. 2010). The elevational range occupied by alpine marmots in the Pyrenees (1300–2800 m above sea level) is similar to in the Alps; however, most populations occur between 1800 and 2400 m above sea level (Herrero et al. 1994a). In the last few centuries, traditional land management in the Pyrenees has resulted in increases in the extent of subalpine grasslands, which have become the primary habitat of marmots (Herrero et al. 1992, 1994a, López et al. 2009a). Alpine marmots can occupy large forest clearings if they provide good visibility (Herrero & García-Serrano 1994, da Ros & Chazel 1997). In the Alps and the Pyrenees, alpine marmots prefer southern exposures (Herrero & García-Serrano 1994, González-Prat et al. 2001, López et al. 2009b), which might have contributed to the rapid expansion of the species into the southern Pyrenees (González-Prat et al. 2001).

In the Pyrenees, populations of alpine marmots became established in the same manner as in other areas where the species was introduced (see Ramousse & Le Berre 1993b, Borgo 2003, Ramousse et al. 2009): in the early stages, alpine marmots often occupy areas that have natural shelters; later, they expand into open areas that have deeper soils (García-González et al. 2006). Rocks provide shelter and are very important when the nascent population is small (Giboulet et al. 2002), particularly when burrows are unavailable (Borgo 2003). A hierarchy of variables influences whether a population becomes established and how it increases (Allainé et al. 1994, Borgo 2003, López et al. 2009b). First, the general features of the environment determine whether a site is suitable for the establishment of a population. If that condition is met, other site-specific features, such as the availability of preferred food types or certain habitat structures like talus, become important in the formation of populations (López et al. 2009b).

In the Pyrenees, introduced alpine marmots might have occupied a vacant ecological niche, as they use space similarly to marmots in the species' native range (Herrero & García-Serrano 1994). Similarities in the climate and habitats in the Pyrenees and the Alps probably facilitated the establishment of alpine marmot populations in the Pyrenees (Herrero & García-Serrano 1994, López et al. 2010).

Structure and dynamics of marmot populations in the Pyrenees

The alpine marmot is a highly social species, and the size and composition of social groups can affect population dynamics (Mann & Janeau 1988, Stephens et al. 2002, Grimm et al. 2003). In the extremely harsh environment that alpine marmots inhabit, ecological factors (e.g. length of the growing season, foods available and quality of hibernacula) and social factors (e.g. social thermoregulation and group size) might strongly influence survival and reproductive success (Arnold 1990b, Allainé 2000, Allainé et al. 2000). The main causes of mortality in marmots are predation and death during hibernation (Arnold 1990b, Nogué & Arthur 1992, Lenti Boero 1999). Infanticide makes up over 50% of juvenile mortality, and so is likely to be an important factor in determining the survival of young of the year (Coulon et al. 1995, Farand et al. 2002).

In the alpine marmot, the family group is the basic social unit, which usually includes a territorial, dominant breeding pair, a variable number of mature subordinates (2–4 years old), yearlings and juveniles (Arnold 1990a, Perrin et al. 1993, Lenti Boero 1994). The average size of family groups did not differ significantly ($Z = -1.48$; $P = 0.140$) between populations in the Pyrenees and those in the western Alps. The average number of young marmots per family group was marginally greater ($Z = 1.94$; $P = 0.053$) in the Pyrenees than in the Alps (Table 1).

Family groups defend territories, which are delimited by scent marking (Mann et al. 1993). The resident pair, especially the territorial male, assumes most of the responsibility for defending the group's home range against adult male intruders (Arnold 1990a). Territories remain relatively stable over time (Mann & Janeau 1988, Lenti Boero 2003). Habitat quality and the presence of neighbouring families can influence the size of a family's home range (Zelenka 1965, Mann & Janeau 1988). In the only study of its kind in the Pyrenees, the average home range of marmots seems to be smaller than the average home range of alpine marmots in the Alps, but small sample size precluded statistical comparisons (Table 1). Overall, the densities of alpine marmot populations were similar in the Pyrenees and the Alps ($Z = -0.40$;

P = 0.678; Table 1), which suggests that the alpine marmot is well established in the Pyrenees.

Potential impacts of alpine marmots on Pyrenean ecosystems

Marmots burrow in soils, and individuals can consume several hundred grams of vegetation a day; consequently, they can have a significant impact on their environments (Armitage 2000). Marmot species are similar in size and, therefore, might have similar energy requirements and impacts on their environments (Armitage 2000). When alpine marmots were introduced to the Pyrenees in 1948, several potential effects were identified, such as alterations of food webs, modifications of the hydrological properties of soils (through burrowing) and interspecific competition with other herbivores (García-González et al. 1985, Canut et al. 1989). Although those effects have been reported in alpine marmot populations in the Alps and in other marmot species, they have not been thoroughly evaluated in the Pyrenean populations. Here, we identify and discuss the potential effects of alpine marmots in their introduced range in the Pyrenees, extending the ideas proposed in previous research and focusing on the main activities (i.e. grazing and burrowing) and roles (i.e. as a prey species and as a vector for parasites and disease) of alpine marmots in mountain ecosystems (Fig. 2).

Marmot foraging behaviour: impacts on vegetation

We found just four studies on the diet of alpine marmots; three of these were conducted in the Alps (Bassano et al. 1996, Massemin et al. 1996, Rudatis & De Battisti 2005), and one in the Pyrenees (Garin et al. 2008). The alpine marmot is primarily herbivorous and consumes a wide variety of plants. In the Spanish Pyrenees, 42 plant species were identified in the diet of alpine marmots (Garin et al. 2008), but forbs contributed the most to their diet (Table 2), probably because of their high nutritional value (Garin et al. 2008), high water content (Stallman & Holmes 2002) and high digestibility (Rudatis & De Battisti 2005, Marinas & García-González 2006). Graminoids were a significant proportion of the diet but were only consumed at the

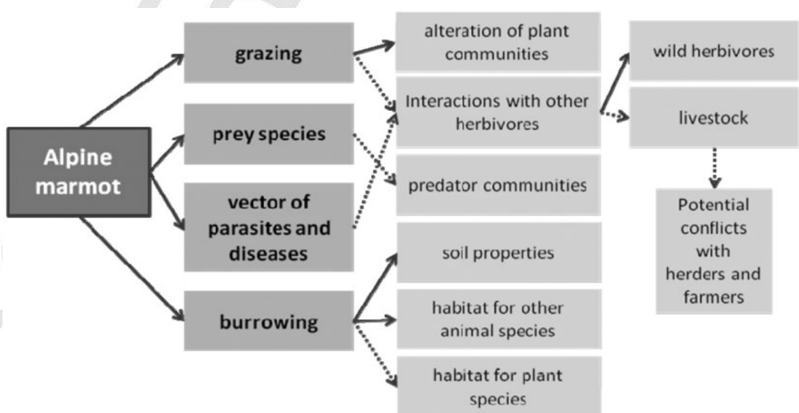


Fig. 2. Potential effects of alpine marmots on the ecosystems they inhabit. Solid arrows indicate effects that have been studied; dotted arrows indicate potential effects that are known to occur in other marmot species.

Table 2. Alpine marmots' diets throughout the active period (May–September) in the Alps and the Pyrenees

		May			June			July			August			September			Overall		
		M	D	O	M	D	O	M	D	O	M	D	O	M	D	O	M	D	O
Alps																			
Italian Alps (Gran Paradiso NP)†		23.0	77.0	–	22.0	78.0	–	3.0	97.0	–	1.0	99.0	–	14.0	86.0	–	12.6	87.4	–
Italian Alps (Belluno province)*‡	A				58.3	41.4	0.3	19.6	80.4	0.0	10.8	88.9	0.3	35.7	63.8	0.6	29.2	64.4	6.4
	B				33.5	66.5	0.0	12.5	86.6	0.9	8.5	91.5	0.0	10.8	88.9	0.3	14.5	74.6	10.9
French Alps (La Vanoise NP)§	A							30.0	70.0	–	34.4	65.6	–	36.1	63.9	–	32.8	67.2	–
	B	79.0	21.0	–	26.0	64.0	–	30.0	70.0	–	56.5	43.5	–	30.0	70.0	–	43.6	56.4	–
	C	39.5	60.5	–	11.0	89.0	–	5.5	94.5	–	11.0	89.0	–	5.5	94.5	–	14.5	85.5	–
Pyrenees																			
Navarre (Larra-Belagoa NR)¶		26.2	72.1	1.7	31.1	67.7	1.2	7.5	91.0	1.5	23.1	76.9	0.0	18.3	80.4	1.3	21.4	77.6	1.0

M, monocotyledons; D, dicotyledons; O, others, including woody plants, fungi and/or invertebrates; –, no data available.
Percentages of fragments found in microhistological analyses of faeces are shown. When studies included more than one population, the populations were treated as independent units and are indicated by capital letters.
*Undetermined fragments were excluded from analyses.
†Bassano et al. (1996).
‡Rudatis and De Battisti (2005).
§Massemin et al. (1996).
¶Garin et al. (2008).

beginning of the growing season (Table 3), when they offer the highest nutritional value (Bassano et al. 1996, Massemin et al. 1996, Rudatis & De Battisti 2005). Minor contributions to the diet came from woody plants, invertebrates, fungi and ferns, and they were consumed primarily in the first few weeks after hibernation (Bassano et al. 1996, Garin et al. 2008).

Given certain physiological constraints linked to hibernation, marmots have to maximize their energy intake and accumulate enough fat during their active period for overwinter survival (Armitage et al. 1976). In the Alps (Zelenka 1965) and in the Pyrenees (Nogué & Arthur 1992, Herrero & García-Serrano 1994), their active period lasts for 5–6.5 months (April to September) and coincides with the short growing period of plants in alpine environments. Therefore, alpine marmots tend to be selective foragers (Bassano et al. 1996, Massemin et al. 1996, Bruns et al. 1999). As in other marmots, the nutrient content of the diet of alpine marmots is affected by plant phenology and availability, and varies throughout the active period (Massemin et al. 1996, Garin et al. 2008). Alpine marmots consume various parts of plants (Massemin et al. 1996, Garin et al. 2008), but at the beginning and end of their active period most of their diet consists of the vegetative parts, i.e. leaves and roots (Bassano et al. 1996, Rudatis & De Battisti 2005; Table 3). Flowers and fruits were mostly consumed in July and August in the Pyrenees (Garin et al. 2008) and in June and July in the Alps (Massemin et al. 1996), during the period of highest flower and fruit production in each of these mountain environments (Körner 1999). A diet rich in flowers and seeds can produce fat deposits with a high proportion of polyunsatu-

Table 3. Diet of alpine marmots in the Pyrenees (after Garin et al. 2008) based on the microhistological analyses of faeces

Botanical family	June	July	August	September
Monocots				
*Poaceae (= Gramineae)**	+	–	0	–
Cyperaceae + Juncaceae	–	0	0	–
Herbaceous dicots				
*Caryophyllaceae**	–	–	–	+
Cistaceae	–	–	–	0
*Asteraceae (= Compositae)**	–	+	+	+
Lamiaceae (= Labiatae)	–	–	–	–
*Fabaceae (= Leguminosae)**	+	+	+	+
Plantaginaceae	+	0	–	–
Polygonaceae	–	–	–	–
Rubiaceae	–	–	–	–
Scrophulariaceae	–	–	–	0
*Apiaceae (= Umbeliferae)**	+	–	+	+
Woody dicots				
Fabaceae (= Leguminosae)	–	–	–	–
Total: mean % (SD)				
Veget	92.3 (2.8)	77.6 (3.2)	73.3 (12.3)	88.8 (5.2)
Reprod	6.9 (3.0)	21.9 (3.0)	25.9 (11.9)	9.2 (6.9)

Only those plant taxa that had a frequency in faeces of >2% are shown. Positive (+), negative (–) and non-significant (0) selection was assessed by comparing marmot diet and plant availability using Jacob's Selectivity Index. Totals are separated into the vegetative parts of plants (*veget*: leaves, stems) and reproductive parts of plants (*reprod*: flowers, fruits, seeds). Asterisks indicate the botanical families which are most abundant in the alpine marmot's diet.

rated fatty acids (Hill & Florant 1999), crude proteins and phosphorus (Marinas & García-González 2006). Some polyunsaturated fatty acids are essential dietary components for marmots that enhance hibernation (Ruf & Arnold 2008; but see Arnold et al. 2011) and are thus critical to survival.

The influence of selective foraging by other species of marmots on the composition and dynamics of plant communities has been demonstrated for *M. olympus* (del Moral 1984), *M. monax* (Swihart 1991), and *M. camtschatica* (Semenov et al. 2001), but we found just two studies on the effects of alpine marmots on vegetation in the Alps (Semenov et al. 2003, Choler 2005). Although marmots consume a small proportion of the plant biomass within their home range (c. 5% in *M. flaviventris*; Kilgore & Armitage 1978), they can have local effects on plant biomass and species composition (del Moral 1984, English & Bowers 1994, Van Staalduinen & Werger 2007, Yoshihara et al. 2009). A moderate level of foraging by marmots may reduce the dominance of common species and, thereby, enhance community diversity (del Moral 1984), but the impacts vary depending on habitat productivity and other factors associated with the scale of the study (Yoshihara et al. 2009), the intensity of the disturbance (Yoshihara et al. 2010b, d) and the overlapping effect of different animals (Yoshihara et al. 2010a). Thus, grazing by marmots is a scale-dependent disturbance that helps to maintain biodiversity in some plant communities subjected to specific management practices (Semenov et al. 2001, Yoshihara et al. 2010b).

Alpine marmots and food webs in the Pyrenees

Alpine marmots are prey for some predators, and their presence might reduce the predation pressure on other prey species such as black grouse *Tetrao tetrix* in the Alps and European hare *Lepus europaeus* in the Pyrenees (Ramousse & Le Berre 1993a). Golden eagles are one of the main predators of alpine marmots and, in the Alps, marmots form a large proportion of their diet (Haller 1982, Pedrini & Sergio 2002). In the Pyrenees, however, predation by golden eagles in the early stages of the introduction did not appear to be a significant source of mortality (Clouet 1982). Today, however, marmots are a large part of the diet of golden eagles (Mañosa et al. 2009). In the Alps, marmots are preyed upon heavily by red foxes *Vulpes vulpes* (Borgo et al. 2009; J. H., personal observation) and, to a lesser extent, by goshawks *Accipiter gentilis* (Perrone et al. 1992, Lenti Boero 1999) and Eurasian lynx *Lynx lynx* (Breitenmoser & Haller 1993, Jobin et al. 2000). In the Pyrenees, golden eagles, foxes and domestic dogs *Canis familiaris* are major predators of alpine marmots (Herrero & García-González 2007; J. H., personal observation).

In the Pyrenees and the Alps, the predators of alpine marmots appear to be similar; however, the effects of marmots on predator populations in the Pyrenees should be investigated, particularly given the marmot's expansion throughout the mountain range and the increases in its population density. The alteration of predator population numbers may have cascading effects on other native herbivores, for example the endangered rock ptarmigan *Lagopus muta* (Figueroa et al. 2009).

Marmots as vectors of parasites and disease

Marmots can be important disease vectors (Bibikov 1992). For example, some marmot species (e.g. *M. bobak*) can act as reservoirs for zoonoses such as the plague (Bibikov 1992, Mann et al. 1993). Most of the diseases carried by other marmot species have not been detected in the alpine marmot (Bassano 1996), so it may not pose a significant risk as a disease vector (Mann et al. 1993), but little is known about the pathology of the alpine marmot, especially about its bacterial and viral diseases.

A variety of endoparasites have been described for the alpine marmot; most of the studies were conducted in the Alps (Manfredi et al. 1992, Prosl et al. 1992, Bassano 1996, Callait 1997). Few ectoparasites have been described from alpine marmot populations in the Alps (Arnold & Lichtenstein 1993). Just two studies of the endoparasitic fauna of alpine marmots have been carried out in the Pyrenees (Gortázar et al. 1996, Riba & Tena 1999), where the marmots might be exposed to foreign parasites or introduce new parasites to the region. Gortázar et al. (1996) found fewer parasites in alpine marmots in the Pyrenees than have been associated with the species in the Alps; although, one was a new record for the species (an unidentified trematode) and others were new to the Pyrenees (*Calodium hepaticum*, *Ctaenotenia marmotae* and *Eimeria spp*., identified later as *E. marmotae* and *E. arctomysi* by Riba & Tena 1999). The effects of those parasites on populations of marmots, and the potential transmission of introduced parasites to other species in the Pyrenees should be investigated. Alpine marmots may act as vectors of soil keratinophillic fungi, some of which can be pathogenic (Gallo et al. 1992), and while some keratinophillic fungi were found in the one study in the Pyrenees, none was pathogenic (Bárcena & Herrero 1994).

Effects of burrowing by alpine marmots

Burrowing by marmots can modify the physical and chemical properties of soils (*M. sibirica*; Van Staalduinen & Werger 2007, Yoshihara et al. 2009), which can have cascading effects on other components of the ecosystem such as plant communities and pollinators (Yoshihara et al. 2010c). In addition, the fossorial activities of marmots can create micro-ecosystems that can support other organisms (Ramousse & Le Berre 1993a). Marmot burrows are used by a variety of animals including small mammals (e.g. *Microtus pennsylvanicus*, *Peromyscus leucopus* and *Blarina brevicauda* in *M. monax* burrows; Swihart & Picone 1995) and endangered carnivores (e.g. *V. corsac* in *M. sibirica* burrows; Murdoch et al. 2009). The burrows of the alpine marmot may provide high-elevation refuges for insects (Pont & Ackland 1995), amphibians, reptiles (e.g. *Bufo bufo* and *Malpolon monspessulanus*; Herrero & García-Serrano 1994) and red foxes (Jordán & Ruiz-Olmo 1988), and temporary shelters for rock ptarmigan (Herrero & García-Serrano 1994). Thus, like other marmot species (*M. sibirica*; Van Staalduinen & Werger 2007, Yoshihara et al. 2009) and other burrowing herbivores that inhabit similar environments (e.g. plateau zokors *Myospalax fontanierii* Zhang et al. 2003), alpine marmots can act as ecosystem engineers.

The alpine marmot in a changing environment

The Pyrenees are the south-western limit of the distribution of alpine marmots. At the limits of a species' distribution, populations face stronger ecological and genetic pressures than they do elsewhere (Hampe & Petit 2005). Although both mountain ranges are within the species' physiological range, global climatic conditions differ between the Pyrenees and the Alps, and are drier and warmer in the former (López et al. 2010). The population dynamics and spatial behaviour of populations at a species' range margins are likely to differ from those of populations near the centre of the species' distribution, which might have important implications for the management of alpine marmot populations in the Pyrenees.

The persistence of alpine marmot populations might be jeopardized by habitat destruction (because of the extreme sensitivity of mountain ecosystems to anthropogenic factors), and by changes in climate and land use (Ramousse & Le Berre 1993a). In Europe, climate change will be expressed largely by an increase in temperature (Anonymous 2007) and by the subsequent advance in the snowmelt season, which is likely to benefit alpine marmot populations by extending the growing season (Mann & Janeau 1988); however, higher temperatures may constrain their daily foraging activities (Türk & Arnold 1988). In addition, some climate change models predict changes in precipitation regimes and, therefore, increases in snow cover in some areas, which might enhance marmot survival during hibernation by ameliorating the conditions in the hibernacula, i.e. by preventing very low temperatures (Arnold et al. 1991). However, changes in precipitation regimes may result in droughts in other areas, which have a negative impact on marmot survival (Armitage 2000).

Changes in land use in European mountain systems associated with the abandonment of traditional grazing activities (MacDonald et al. 2000) might lead to an increase in shrub encroachment and forest regeneration and to a subsequent reduction in the amount of habitat suitable for alpine marmots. Indeed, the history of the distribution of the alpine marmot after the ice ages was influenced by the availability of suitable habitats and the development of forests (Zimina & Gerasimov 1973), as marmots disappeared from areas that did not provide suitable habitats. Given the location of the Pyrenees, marmot populations there will be among the first to be affected by such changes. In fact, uphill trends in the treeline and shrub encroachment have already been reported in the Pyrenees (Camarero & Gutiérrez 1999). Thus, it appears that changes in land use are likely to have a negative effect on alpine marmot populations in the Pyrenees.

CONCLUSIONS AND FUTURE DIRECTIONS

Sixty years after their introduction, alpine marmots seem to be well established in the Pyrenees. It appears that similarities between the environment (e.g. climate, habitat) in the species' native range and in the regions where it has been introduced favoured the establishment of alpine marmot populations in the Pyrenees (López et al. 2010). Since the 1980s, the species has extended its distribution in the Pyrenees (García-González et al. 1985; Fig. 1); however, information on the abundance of alpine marmots in the Pyrenees is limited. Nevertheless, population structure and densities in the Pyrenees are similar to those in populations within the native range in the Alps, so we can hypothesize that performance of alpine marmots in the Pyrenees is good.

Despite the potential effects on Pyrenean ecosystems of the introduction of the alpine marmot, limited information is available on the ecological impact of the species. Impacts can be predicted from the few studies conducted within the alpine marmot's native range, and mainly from those describing the impacts of other marmot species through grazing, burrowing and through their role as prey or vector of parasites and diseases. The role of alpine marmots as ecosystem engineers in alpine environments in the Pyrenees should be investigated further, because this research will provide useful insights for the management of the species and the conservation of the mountain grasslands it inhabits.

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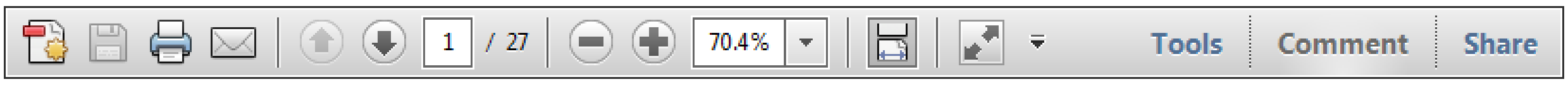

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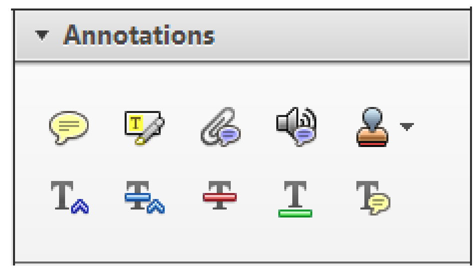

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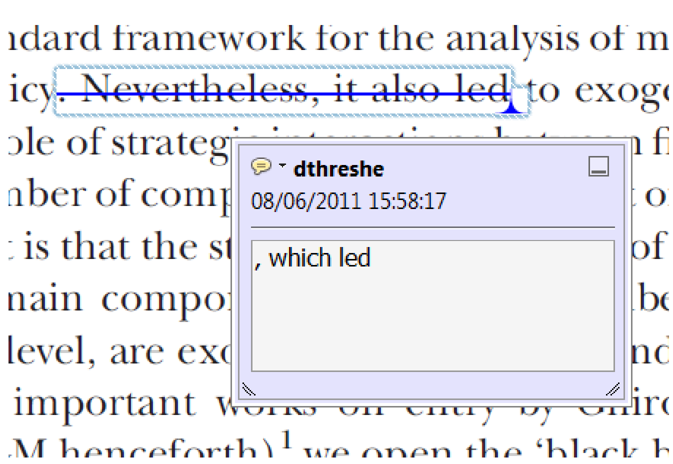

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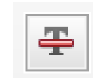

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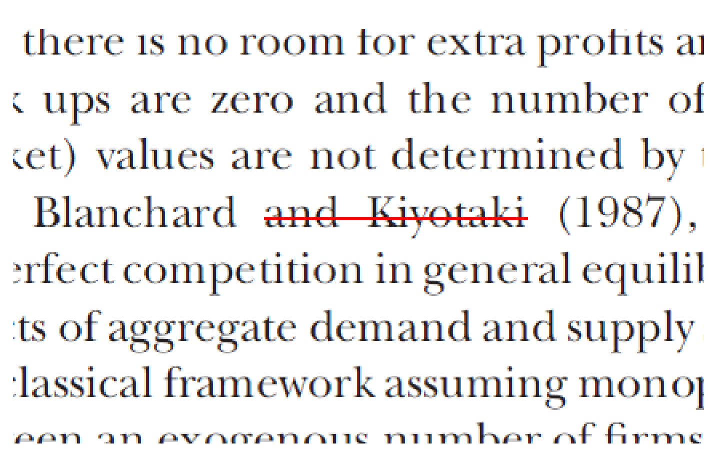

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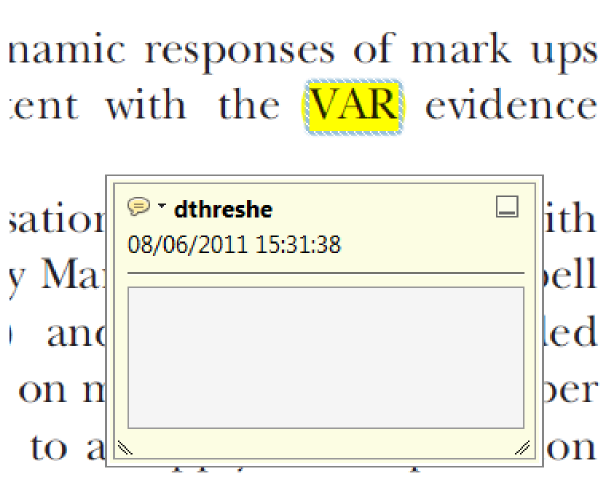

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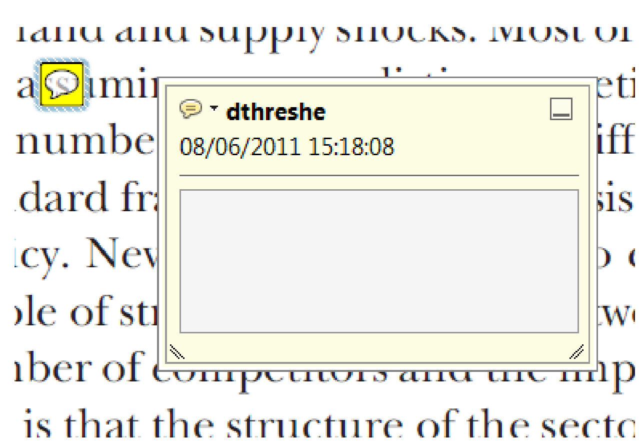

USING e-ANNOTATION TOOLS FOR ELECTRONIC PROOF CORRECTION

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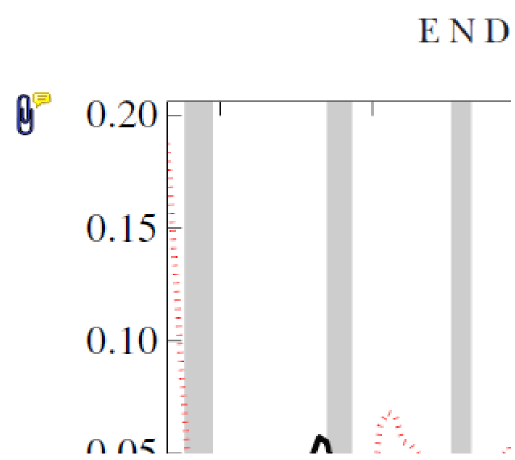

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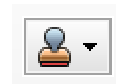

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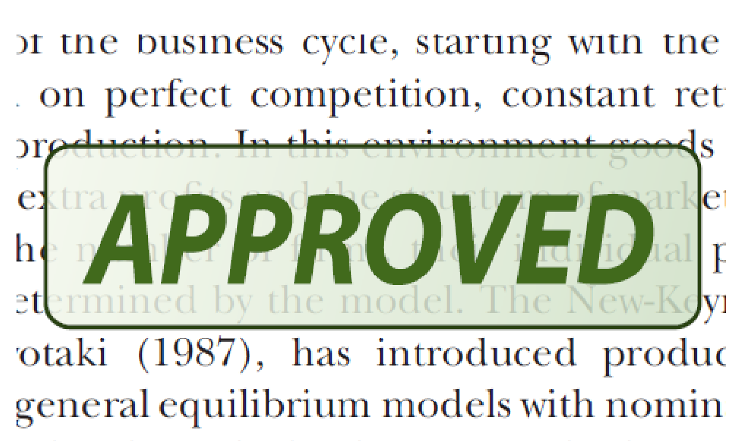

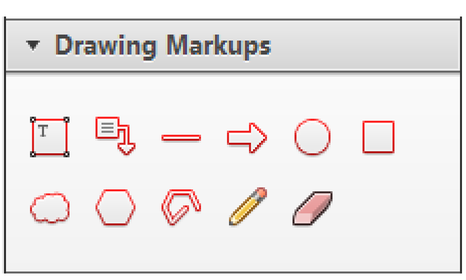

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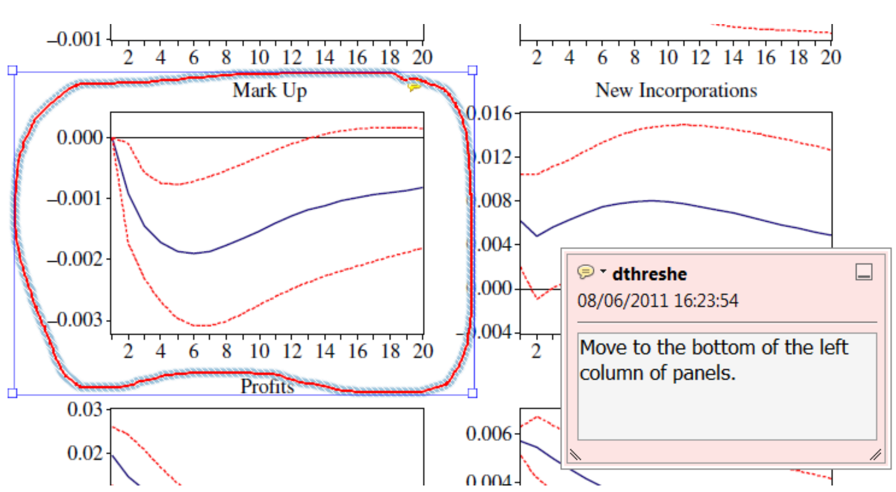

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