Chapter 19

Bears in Human-Modified Landscapes: The Case Studies of the Cantabrian, Apennine, and Pindos Mountains

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Introduction

Brown bears *Ursus arctos* were historically persecuted and almost eradicated from Southern Europe in the twentieth century as a result of hunting and direct persecution (Zedrosser et al. 2011; Martínez Cano et al. 2016). The effects of human-induced mortality were exacerbated by other threats, such as habitat loss and fragmentation, due to the expansion of human populations (Swenson et al. 2000). As a result, nowadays there are only small, fragmented populations of bears in Southern Europe, where brown bears frequently inhabit human-modified landscapes. These areas are characterized by the widespread presence of people and infrastructures, which potentially have ecological impacts on bears. The close coexistence of brown bears and humans generates multiple human-driven disturbances (Ordiz et al. 2017) and causes bear mortality (Bischof et al. 2009), affecting the distribution, demography, behavior, and viability of bear populations (Penteriani et al. 2018a; Zarzo-Arias et al. 2018).

Brown bears in the Cantabrian (north-western Spain), Apennine (central Italy), and Pindos (north-western Greece) mountains (Figure 19.1) represent three examples of small and threatened bear populations in human-modified landscapes (Figure 19.2). Most of their range is characterized by high human densities, widespread agricultural activities, livestock raising, and urban development, connected by dense networks of transport infrastructures (Penteriani et al. 2020; Mateo-Sánchez et al. 2016). This has resulted in a reduction of continuous habitat suitable for the species (Martínez Cano et al. 2016). Here, we summarize the past and present histories and fates of these three populations as examples of how the coexistence of bears and people in human-modified landscapes can take different turns depending on human attitudes.

Cantabrian Bears, the Partial and Ongoing Recovery of a Population

Brown bears in the Cantabrian Mountains represent the westernmost population of the species' range in Europe. Of the four isolated brown bear populations in Western Europe – i.e. Italian Central Apennines and Eastern Alps, Pyrenees (southern France and north-eastern Spain), and Cantabrian – the latter represents the only population exhibiting a natural recovery, with no reintroduction of bears from other populations. The decline of this population, which was already pronounced in the 1960s and 1970s, continued even after its protection in 1973, when population assessments estimated the presence of <100 bears separated in a western and an eastern subpopulation. Indeed, these two subpopulations were already disconnected at the beginning of the twentieth century by a 50–100 km wide strip of land, with bears in the two subpopulations declining in number until the mid-1990s (Palomero et al. 2007; Gonzalez et al. 2016). In the period 1982–1995, the western population was estimated at 50–60 bears and showed an annual decrease of 4–5% (Wiegand et al. 1998), while the eastern subpopulation was estimated in 1990 at only 20–25 bears (Palomero et al. 1993). Although concerns over an imminent extinction were expressed in the mid-1990s (Wiegand et al. 1998; Martínez Cano et al. 2016), and despite negative prospects (Wiegand et al. 1998; Naves et al. 2003a), the Cantabrian brown bear population has increased, mainly in the western part of the Cantabrian Mountains (Palomero et al. 2007; Pérez et al. 2010). It has been estimated that during the first decade of this century the western subpopulation has increased annually by 7.7% (Palomero et al. 2007).

Today, brown bears in the Cantabrian Mountains continue to show a positive trend, there is sign of connection between the two subpopulations, and reproduction has been stable during the last 30 years, at least (Pérez et al. 2010; Gonzalez et al. 2016; Penteriani et al. 2018c). A capture–mark–recapture population estimate using genetic data carried out in 2006 found that the western part of the population represented approximately 90% of the entire population, with 203 bears (confidence interval CI 95% = 168–260) in the west and only 19 bears (CI 95% = 12–40) in the east (Pérez et al. 2014). Despite the positive trends in the west, the eastern subpopulation is showing a substantially smaller increase (Martínez Cano et al. 2016).

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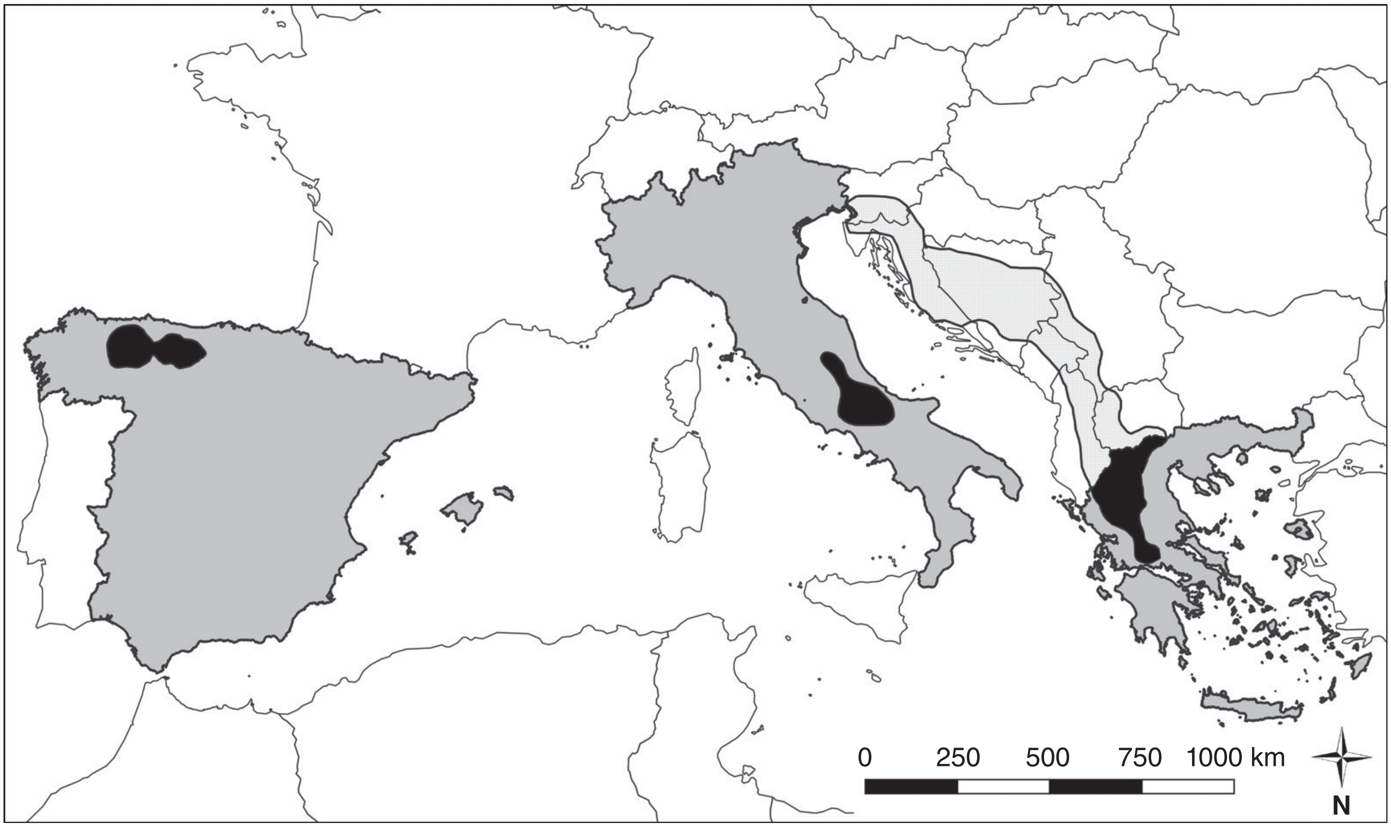

Figure 19.1 The distribution (black areas) of the Cantabrian (north-west Spain), Apennines (central Italy), and Pindos (north-west Greece) brown bear populations. The Pindos population is part of the bigger Dinaric-Pindos population (shaded in light gray) outside Greece.

The number of females with cubs, a proxy of the population trend, has also exhibited a more rapid increase in the western subpopulation than in the eastern one, e.g. 34 vs. 6 females with cubs in 2016 and an average of 25 vs. 4.3 females with cubs during the 10-year period 2007–2016 (Figure 19.3A). The Cantabrian brown bear population shows a relatively high reproductive rate (Penteriani et al. 2018c): (a) mean litter size is significantly larger in the west (1.8 ± 0.2 cubs) than in the east (1.3 ± 0.6 cubs), with litter size for the whole Cantabrian Mountains being 1.6 ± 0.3 cubs; (b) interannual variation in litter size is not significant for the western and the eastern sectors, although in the east interannual differences are more marked (Figure 19.3B); (c) apparent mean cub mortality per female per year is 0.1 ± 0.5 cubs; and (d) estimated reproductive rate for the population is 0.7 young born per year per reproductive adult female. The estimated reproductive rate for the Cantabrian population is among the highest recorded for brown bears (from 0.23 to 0.96; reviewed by Steyaert et al. 2012), which might be due to the high habitat quality of the Cantabrian Mountains (Martínez Cano et al. 2016). It is worth noting here the similarity in reproductive traits between the Cantabrian and the Apennine brown bear populations (Tosoni et al. 2017a). Indeed, both the mean litter size (1.9 cubs in the Italian population and 1.8 in the western Cantabrian Mountains) and litter size proportions for one, two, and three cubs were similar: 33%, 56%, and 11% for the Cantabrian brown bears, and 26%, 55%, and 19% for the Apennine bears, respectively. However, despite similar reproductive parameters, the trends of these two populations have been very different over the last three decades (see The Apennine bears, a demographic stagnation lasting several decades).

In the Cantabrian Mountains, brown bear mortality associated with vehicle accidents is rare and illegal poaching, the most common driver of human-induced bear mortality (Palomero et al. 2007), may have declined in recent decades, resulting in the positive trends exhibited by this population (Gonzalez et al. 2016). A series of management actions beginning in the early 1970s, which has intensified since 1989 with the initiation of several recovery plans, may partly explain the recovery of this population (Martínez Cano et al. 2016). The initiatives that have probably contributed most to the current positive trends of this bear population are: (1) increased monitoring and effective persecution of bear poaching; (2) establishment and enforcement of protected areas; and (3) establishment of compensation programs for bear damages.

However, apart from the varying reproductive rates, the contrast in population growth between the western and eastern subpopulations might suggest: (a) higher mortality rates in the eastern subpopulation; (b) lower population growth rates in the eastern subpopulation due to the smaller number of adult

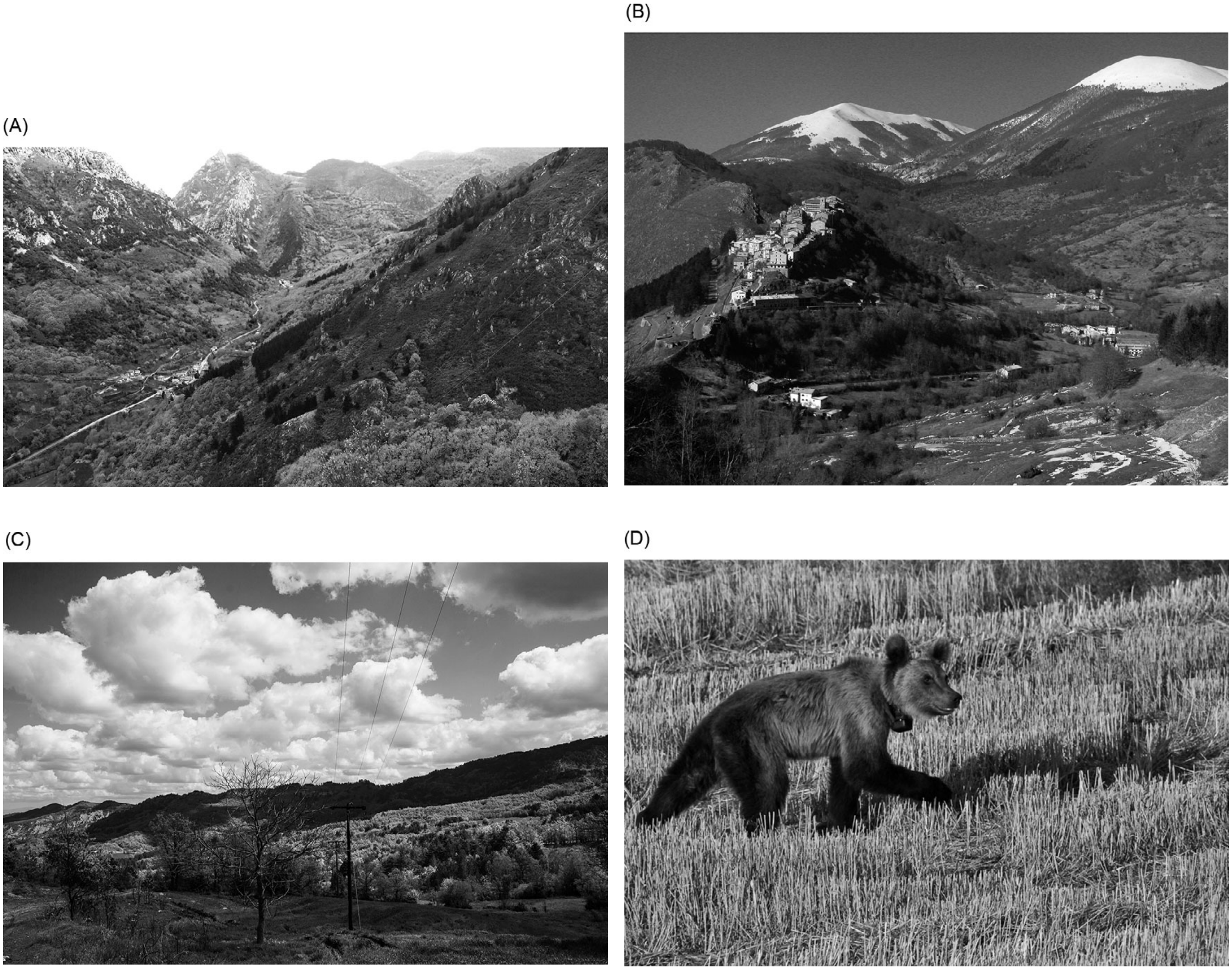

Figure 19.2 Brown bears in human-modified landscapes: three examples of bear habitats with intense anthropogenic influence in the Cantabrian Mountains (A; photo by V. Penteriani), the Apennines (B; photo by P. Ciucci), and the Pindos (C; photo by A. Karamanlidis), as well as a brown bear in a mown wheat field in the Pindos (D; photo by A. Karamanlidis).

females compared to the western one; and (c) limited bear dispersal from the larger, western subpopulation. In fact, some studies have suggested a narrow connection between the two subpopulations, which seems to be maintained nowadays in spite of the development of transportation infrastructures between the two areas (García et al. 2007; Pérez et al. 2010; San Miguel et al. 2012; Mateo-Sánchez et al. 2014b). However, even if female philopatry has been highlighted as one of the potential causes of the slow recovery of the eastern sector, with little or no flow of females moving from west to east (Palomero et al. 2007), this may not solely explain the apparent lower reproductive rate or higher mortality in this subpopulation. During the last 40 years, the eastern subpopulation has always been 1/3–1/4 smaller than the western one (Palomero et al. 2007; FAPAS/FIEP 2017). If habitat use by the two brown bear subpopulations of the Cantabrian Mountains offers only limited help in explaining the evolutionary differences in population size and fecundity exhibited by the two subpopulations (Lamamy et al. 2019), other factors might be acting on the different ways in which these subpopulations have evolved over the last few decades. Indeed, the higher human presence and more fragmented forest habitat in the west (Lamamy et al. 2019) is not consistent with the higher growth rates of this subpopulation. Thus, human practices and attitudes toward bears might be undermining bear recovery more than the natural landscape, and suspicions point to direct human influence on the different trends exhibited by the two bear subpopulations. For instance, the persistence of poaching and/or bad practices during hunting might be more pronounced in the eastern sector of the Cantabrian Mountains, resulting in higher bear mortality. Less surveillance of eastern areas together with less-effective antipoaching measures might be the main causes of the low growth of the eastern subpopulation. Earlier studies have also associated the slower recovery of the eastern

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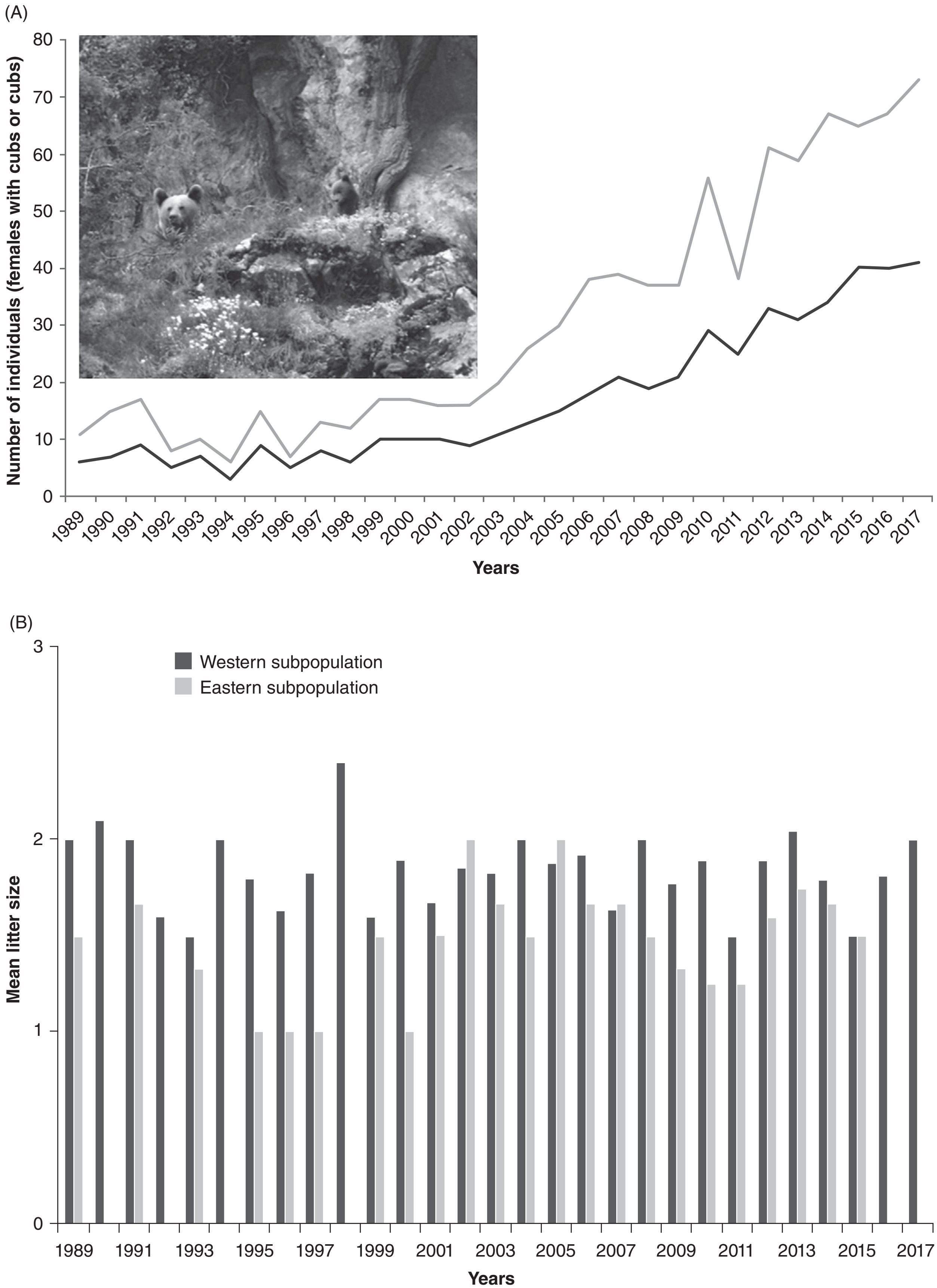

Figure 19.3 Characteristics of the brown bear population inhabiting the Cantabrian Mountains. (A) Trends of the number of females with cubs (black line) and number of cubs produced per year (gray line) from 1989 to 2017. (B) Interannual variations in brown bear mean litter size (number of cubs) for the western (1989–2017) and eastern (1989–2015) subpopulations.

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subpopulation with the existence of low-quality food items in the eastern sector of the Cantabrian Mountains (Clevenger et al. 1992; Naves et al. 2003a, 2006).

Brown bear habitat suitability in the Cantabrian Mountains is determined by multiple factors at a range of scales, from local resources such as quality forest cover and food resource availability within the home range to the avoidance of human disturbance at broader spatial scales (Mateo-Sánchez et al. 2014a, 2016). To ensure the long-term viability of the species, it is critical to not only ensure the conservation of their habitat areas, but also maintain an adequate level of connectivity among them to allow the movement of individuals and genes between both subpopulations and toward new available areas of suitable habitat. Landscape features have important influences on bear movements, with areas with high forest canopy cover and shrubland cover promoting successful movements, while, on the contrary, intensively human-modified cover types present considerable resistance to species movements. Dispersing bears are more flexible in their movement behavior and less constrained by landscape conditions than when selecting areas as stable habitat, achieving long-distance movements through low-quality habitat areas even with a high human footprint (Mateo-Sánchez et al. 2015a, 2015b). This dispersal plasticity, together with the notable population growth and the implemented actions to improve landscape matrix permeability (e.g. LIFE+ programs), seem to have led to a certain level of recovery of interpopulation connectivity after a considerable period of isolation (Pérez et al. 2010, 2014). In fact, current evidence seems to show that dispersal movements between subpopulations are increasing (Pérez et al. 2010, 2014) and their frequency may lead to a sufficient amount of gene flow between populations to mitigate potential deleterious effects of isolation and inbreeding (Mills & Allendorf 1996; Vucetich & Waite 2000). Therefore, facilitating adequate levels of dispersal between the two populations should be a priority in connectivity strategies. Thus, one of the current main challenges is to foster a steady expansion of the species range into available areas that were part of the historic distribution of brown bears in the Cantabrian range and neighboring areas.

Finally, if the current positive trends continue in the Cantabrian Mountains, a large amount of habitat still seems available for range expansion of the species (Martin et al. 2012; Scharf & Fernández 2018). For example, brown bears currently occupy about 2400 km^2 in Asturias, a region at the core of the Cantabrian Mountains, while about 5000 km^2 (approximately half of the region) have been identified as suitable bear habitat (Zarzo-Arias et al. 2019). Most of the suitable areas in the western part of the region are already occupied (77% of identified areas), 41.4% of them occurring inside protected areas. Therefore, there are relatively few good areas for further bear expansion in this part of the region, although there are suitable areas in surrounding regions. However, in the eastern part of Asturias, 62% of the land is classified as suitable habitat, representing 44.3% of the total area identified as suitable bear range in the whole region. Forty-one percent of all expansion areas (suitable areas outside the current bear range) are within protected areas (Zarzo-Arias et al. 2019) in Asturias.

The Apennine Bears, a Demographic Stagnation Lasting Several Decades

Brown bears *Ursus arctos marsicanus* in the Apennines survive in a relict and isolated population of about 50 bears, including cubs (Gervasi et al. 2012; Ciucci et al. 2015), critically endangered both at the European and the national level (Ciucci et al. 2017). In fact, the risk of extinction in the next 100 years has been estimated to be between 11% and 21% (Gervasi & Ciucci 2018). Although the taxonomic status of this bear population is debated (Ciucci & Boitani 2008; Colangelo et al. 2012), their long-term isolation from other brown bear populations makes Apennine bears a unique evolutionary and conservation unit, based on genetic, morphological, and behavioral traits (Loy et al. 2008; Ciucci & Boitani 2008; Colangelo et al. 2012; Benazzo et al. 2017). Genomic data suggest that this population, originally spread throughout most of the Apennine range, lost connectivity with other brown bear populations many years ago, when forest clearing was very intense (Benazzo et al. 2017). More recently, the distribution of Apennine bears declined progressively in the seventeenth century, but most of their range contraction likely took place over the past 200 years, mainly due to human persecution and changes in land-use practices. The first effort to evaluate the census size of this population was undertaken in 1970, when 70–100 bears were estimated (possibly overestimated) within an area of about 500 km^2. In the last few decades, further estimates produced numbers between 40 and 80 individuals, a size close to the current one (Ciucci & Boitani 2008). Nowadays, the population is structured in a core and a peripheral range, the former comprising the historical Abruzzo Lazio and Molise National Park (PNALM) and surrounding areas, and the latter largely including a limited number of wandering bears, mostly males (Ciucci & Boitani 2008). Recently, the presence of bears in the peripheral areas, including females with cubs (Ciucci et al. 2017; Morini et al. 2017), has been increasingly reported (Van Gils et al. 2014; Morini et al. 2017), although it is still uncertain if this reflects an actual tendency toward range expansion or if this is the result of increased monitoring efforts (Ciucci et al. 2017). Nevertheless, these peripheral areas of bear presence, both inside and outside protected areas, are crucial for species conservation and management (Falcucci et al. 2009; Ciucci et al. 2017; Morini et al. 2017) and indicate that some connectivity with the core area exists, mainly toward the north-west, east, and north-east. Despite long-term protection and the availability of suitable habitat at the landscape scale (Posillico et al. 2004; Falcucci et al. 2009), the distribution of the Apennine population has not increased during the last several decades, nor have reproductive nuclei been stably established outside the core area (Ciucci et al. 2017).

Figures of minimum known mortality indicate that protection of Apennine bears has not been as effective as desirable for such a small bear population (reviewed by Ciucci & Boitani 2008). For example, between the establishment of the PNALM in 1923 and 1974, at least 99 bears were killed, with a higher rate of known mortality (2.4 bears/year) during the final decade of this period. Higher rates (3 bears killed/year) were reported in the following decade, when poaching and vehicle collisions accounted for 60% of known bear mortalities. However, a peak in bear mortality was recorded between 1980 and 1985, when a minimum of 32 bears were killed (5.3 bears/year), probably due to an increase in poaching. During the period 1991–2002, known bear mortality averaged 2.5 bears killed/year (with half of killed bears being female), whereas in more recent years the minimum known mortality totalled five bears (2003–2007). Three of these were killed in a single poisoning event in the core of the PNALM, most likely motivated by conflicts over livestock depredation. In addition, 16.4% of dead bears were found outside the core area (PNALM 2018), thus further hindering any attempts by young bears to expand the range of the population. Of all reported bear mortalities, 84% have been from illegal or accidental killing by humans, with poaching (mainly shooting and poisoning) being one of the primary causes of reported bear fatalities. Other causes of mortality were unintentional, but still related to the bears living in a human-modified landscape, i.e. vehicle and train accidents, mortality from snares or poison baits illegally set, and diseases (e.g. brucellosis, tuberculosis) potentially transmitted by pets and livestock. Diseases or reduced reproduction could represent an underestimated cause of mortality for Apennine bears (Ciucci & Boitani 2008); some bears have recently tested positive for canine parvovirus and canine distemper, and they can also contract *Brucella*, which can depress reproduction. In 2014 an adult female bear died of tuberculosis likely transmitted by cattle (L. Gentile, PNALM Veterinary Service, personal communication).

Currently, the bear range is estimated at 5422 km^2 across the central Apennines, mostly concentrated in a southern area (4923 km^2, 90.8% of the estimated distribution) that largely overlaps with the stronghold of the species over the last few decades (Ciucci et al. 2017). With a few exceptions (see above), reproducing female bears (1–6 family groups per year from 2005 to 2014; Tosoni et al. 2017b) occupy an area of 1460 km^2, completely encompassed within the main bear distribution. Almost 60% of the current bear range is included within protected areas. Mean litter size is 1.9 ± 0.7 (range = 1–3) cubs and the mean interval between litters is 3.7 years, with the age of first reproduction between 5 and 6 years, corresponding to a reproductive rate of 0.24 (95% CI = 0.07–0.59) (Tosoni et al. 2017a). The combination of a relatively long interbirth interval and several non-reproducing adult female bears may contribute to the relatively low reproductive rate of Apennine bears as well as partly explain the slow recovery of this population, which may also be characterized by relatively high cub mortality (Tosoni et al. 2017a; Gervasi et al. 2017). Although no clear demographic evidence of inbreeding depression has been obtained thus far, genomes are characterized by long stretches of homozygosity, and in general the genetic diversity of this population is also very low for quantitative traits (Lorenzini et al. 2004; Benazzo et al. 2017). Estimated levels of inbreeding are high, as are the number of fixed mutations predicted as deleterious that accumulated through drift during the long period of isolation of this small population (Benazzo et al. 2017). Therefore, in addition to the high levels of human-related mortality, it cannot be excluded that the relatively low reproductive performance and cub survival in Apennine bears may be due in part to genetic factors. It is interesting to note that genetic variation is retained at immune system and olfactory receptor genes, i.e. genes crucial for interacting with the environment (Benazzo et al. 2017).

Thus, Apennine bears are still highly endangered, i.e. they are a small, isolated population with limited genetic diversity and a high genetic load, with a restricted distribution of reproducing females, despite: (a) a female productivity in the core population that seems compatible with population growth (although in the lower spectrum of the reproductive performance of other non-hunted brown bear populations in Europe; Tosoni et al. 2017b; Gervasi & Ciucci 2018); (b) a relatively high density in the core range (about 40 bears/1000 km^2; 95% CI = 37–51), which, along with dietary analyses, indicate that habitat productivity is currently adequate for bears (Ciucci et al. 2014, 2015); and (c) habitat suitability and connectivity that do not seem limiting at the landscape scale (Falcucci et al. 2008, 2009; Maiorano et al. 2017). It is remarkable that, although most of the bear range falls within protected areas and productivity is high, this bear population has not grown in the last few decades, as has been the case for the Cantabrian and Pindos bears. Although bears in the Apennines have been legally protected since 1939 (well before their counterparts in Spain or Greece), they have not been efficiently supported in the last several decades by increased surveillance or protected from poachers. Furthermore, although there are several protected areas in the Central Apennines that largely overlap with suitable bear habitat, the landscape appears interspersed with ecological traps, i.e. areas where habitat suitability is high, but intimately associated with a high risk of human-caused mortality (Falcucci et al. 2009; Penteriani et al. 2018a). Therefore, as in the case for the eastern Cantabrian subpopulation, we suggest that the lack of population recovery in the Apennines is largely due to human-related mortality. In a densely populated country such as Italy, brown bear damage to human interests such as livestock or crops can be substantial and yet difficult to mitigate due to cultural and social resistance, especially outside the historical stronghold of the species, where attitudes are generally more positive and tolerance toward bears is higher. Genetic factors may play a role, especially in the near future, but their negative effects on survival and fecundity are probably still limited and require further investigation.

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Even if habitat degradation is critical for the Apennine population, it is perhaps secondary to human-caused mortality (Ciucci & Boitani 2008; Falcucci et al. 2009). Antipoaching campaigns were not effective and, as a result, total mortality might have been too high to allow population recovery given the current reproductive performance. Indeed, the recent dynamics in bear range and the number of bears do not offer any clear indication of population recovery, suggesting that the Apennine brown bear may have persisted at dangerously small numbers over the last four decades. Despite protection, the current status of the Apennine brown bear population highlights how, at small bear population size, effective long-term conservation can be problematic. Across the central Apennines, including protected areas, even if human density is relatively low when compared with the rest of Italy, livestock grazing, timber harvesting, hunting (outside protected areas only), vehicle traffic, tourism, and other recreational activities are still not regulated in order to reduce their potential impact on bears (Ciucci & Boitani 2008; Falcucci et al. 2009). These additional factors have the potential to greatly influence bear occurrence, movements and feeding activity, reproduction and the survival of individuals (Ciucci et al. 2014). Consequently, the spatial scale of species conservation and management should be consistent with the scale at which human pressure and threats occur, a process which is not aided by the fragmentation of administrations in charge of bear management and conservation.

Understanding the Recovery of Brown Bears Living Next to Humans: the Case of the Pindos Mountains

In ancient times, and up until the sixteenth century, the species was widespread throughout mainland Greece, including the Peloponnese Peninsula. Following this, it appears that the brown bear range decreased dramatically from the eighteenth century onward, mainly due to the systematic persecution of the species and habitat alteration (Mertzanis 1999 and references therein). The Pindos bear population is attached to the larger Dinaric-Pindos biological population covering nine countries of the western Balkan region (Kaczensky et al. 2013).

During the period 1985–2007 the Greek brown bear population appears to have shown (especially in Pindos) small but progressive increases in population and range sizes. It is estimated that, in the mid-1990s, the total occupied range covered 13,500 km^2 and consisted of two non-communicating population nuclei in the north-western (a.k.a. Pindos population) and north-eastern (a.k.a. Rodopi population) parts of the country with a minimum population size of 130 individuals (Mertzanis 1994, 1999, 2000). Ten years later a recovery of the species was recognized, with the total population estimated to number up to 260 individuals over a total range of 21,300 km^2 (Mertzanis et al. 2009). Acknowledging the critical status of the brown bear in Greece, the species was considered "endangered" in the Red Data Book of Greece and was afforded strict protection by national and international legislation (Mertzanis et al. 2009). To alleviate human–bear conflicts, a compensation system for damages to livestock, apiaries, and crops was also established (Karamanlidis et al. 2011).

Since the beginning of this century, however, brown bears in Greece have been showing clear signs of range, genetic, and demographic recovery (Karamanlidis et al. 2015, 2018; Bonnet Lebrun et al. 2020), especially in the Pindos part of their range. These recoveries have been partly facilitated by specific adaptations by bears in their activity rhythms (De Gabriel Hernando et al. submitted a) and habitat selection patterns (De Gabriel Hernando et al. submitted a, submitted b), together with the rewilding of areas after rural abandonment by humans.

Range Recovery

A comparison between data on bear presence collected from 2004 to 2016 (within the framework of a citizen science program) and the distribution of brown bears in Pindos (Mertzanis et al. 2009) indicates that in the last ~15 years the range of the brown bear in the Pindos Mountains might have increased by as much as 100% (Bonnet Lebrun et al. 2020). This is in accordance with opportunistic, extralimital sightings that have occurred during this time (Mertzanis et al. 2005; Karamanlidis et al. 2008). The current distribution of brown bears in Greece includes recolonized former range areas and is characterized by (a) bears at lower elevations (415 m lower), (b) higher coverage by primary (>175% more) and secondary roads (100% more) as well as agricultural areas (22% more) in bear habitat, and (c) lower coverage by mature forests (25% less) in areas inhabited by bears, compared to that of the past, indicating a recolonization of primarily cultural landscapes. The ability of brown bears to recolonize cultural landscapes in Greece is most likely explained by the behavioral plasticity of the species (Ordiz et al. 2014) and the decrease in agricultural activities in less-productive areas as a consequence of the general rural abandonment, allowing a progressive naturalization of these areas (Mertzanis et al. 2009). Extensive habitat suitability analyses (Mertzanis et al. 2008, 2011) indicate that only a certain percentage of suitable bear habitats in Pindos is currently under protection within the framework of the Natura 2000 network of protected areas (Bonnet Lebrun et al. 2020) and from that, only 33% of the Natura 2000 areas implement specific management actions for the conservation of the species. However, according to very recent developments, the Hellenic Ministry of Environment and Energy has decided to affiliate all Natura 2000 sites into 37 enlarged protected areas and to conduct specific environmental studies with subsequent conservation benefits for the species. Nowadays, bear observations are often recorded in areas with highly suitable habitat currently not protected at all, thus creating a new "conservation reality" for the species in the country, which dictates a re-evaluation of the national management and conservation priorities for brown bears in Greece (Bonnet Lebrun et al. 2020).

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Genetic Recovery

In 2002 a large-scale, nation-wide effort was initiated to understand the genetic processes associated with brown bear recovery in Greece (Karamanlidis et al. 2018), through the evaluation of population structure, genetic diversity, and gene flow. The results of the study indicated a clear distinction between the bear populations in the Pindos and Rodopi mountain ranges. Bears in the Rodopi Mountains, which belong to the large East Balkan population (Frosch et al. 2014), are separated from bears in Pindos by a great distance and partially unsuitable habitat, and clearly stand out as a separate population in population structure analyses. Mitochondrial DNA and microsatellite analysis indicated a further genetic distinction of the Pindos population, separating the bear population into four core areas, i.e. the Mountains of Vitsi-Varnoundas, Northern Pindos, and Central/Southern Pindos. This distinction accords with the hypothesis that isolation at the edge of a species' range favors genetic substructuring (Schaal & Leverich 1996), with this structure likely appearing when bear populations in Pindos survived in two small, isolated fragments.

The legacy of the demographic history of bears in Greece is also discernible in their genetic diversity. As is the case for neighboring populations in Bulgaria (Frosch et al. 2014), bears in Rodopi have high genetic diversity, comparable to that found in the large population in the Carpathian Mountains (Graban et al. 2013). On the other hand, the genetic diversity of bears in western Greece is the lowest recorded in the Dinaric-Pindos population (Skrbinšek et al. 2012), but higher than that recorded in the Apennine bear population (Ciucci & Boitani 2008). Finally, information on population genetics indicates an asymmetric, primarily male-mediated, gene flow among subpopulations in Pindos, which is indicative of a population recovery process through reconnection of previously isolated population fragments (Karamanlidis et al. 2018).

Demographic Recovery

The four core areas identified in the genetic study served as the main sampling areas for studying the demographic recovery of brown bears in Pindos between 2002 and 2010, using a combination of non-invasive and invasive genetic sampling (Karamanlidis et al. 2007, 2010; Tsaparis et al. 2014). Sixty-eight (Vitsi-Varnoundas; density: 54 bears/1000 km^2), 53 (Northern Pindos; 50 bears/1000 km^2), 51 (Central Pindos; 51 bears/1000 km^2), and 10 (Southern Pindos; 10 bears/1000 km^2) brown bears were estimated on average over the study period, which amounts to 182 individuals per year for all sampling areas combined and a conservative estimate of >400 bears for the entire Pindos population (Karamanlidis et al. 2015). This is indicative of a significant population recovery of the bear population in Pindos and is consistent with large carnivore population recoveries throughout Europe (Chapron et al. 2014). Bear densities obtained in the four sampling areas in Pindos were the lowest recorded for the species in the Dinara-Pindos population (Huber et al. 2008; Jerina et al. 2013) and are consistent with the assumption of a Dinara-Pindos population with a core population in the North and extending towards the South (Kaczensky et al. 2013).

Behavioral Adaptations

The range, genetic, and demographic recovery of bears in Pindos has also likely been facilitated by specific behavioral adaptations that enable bears to survive in human-modified landscapes. As it occurred during the recovery of brown bears in Scandinavia (Kindberg et al. 2011), bears in Pindos have shown high levels of behavioral plasticity as a response to the rapidly changing and ecologically challenging environment they inhabit. For example, the activity of adult bears is mainly nocturnal, enabling them to avoid human disturbance (De Gabriel Hernando et al. 2020). Similarly, bear habitat preferences revealed efforts to avoid human disturbance. Also, habitat use had a clear circadian pattern: in general, proximity to human-related habitat features (e.g. intensive crops, naturalized crops, human settlements, road networks, and unpaved roads) was higher at night, whereas proximity to natural habitat features, such as forests, shrublands, high altitudes, and areas with rough terrain was higher during the day for all sex/age classes (De Gabriel Hernando et al. in review).

Despite the population recovery exhibited by the brown bear population in Pindos, the fate of the species has not yet been totally secured. Several threats still compromise the recovery of bears despite legal and institutional protection. These threats include human-caused mortality, e.g. poaching (Mertzanis 2000; Mertzanis et al. 2009), vehicle collisions (Karamanlidis & Mertzanis 2004), retaliatory killing for damage to property (Karamanlidis et al. 2011), and habitat loss, fragmentation, and alteration at a range scale, e.g. construction of major highways (Karamanlidis et al. 2012a, 2012b).

What Can We Learn from Past and Present Histories of Small and Endangered Bear Populations in Human-Modified Landscapes?

The diverse situation, from ongoing recovery to apparent stagnation, of some brown bear populations and subpopulations in human-modified landscapes demands an improvement of our knowledge on how this species is able to coexist with humans (Carter & Linnell 2016) and, in turn, what effects human presence and activity may potentially have on them. This is particularly important in areas with recovering but still endangered brown bear populations (Treves & Karanth 2003; Ordiz et al. 2013), which inhabit areas with suitable habitat surrounded by greater human encroachment, thus creating scenarios that may become ecological traps (Naves et al. 2003b; Penteriani et al. 2018a; Scharf & Fernández 2018).

The case of the Cantabrian bear population is particularly noteworthy from a conservation perspective as human-induced mortality appears to have decreased, the potential for population recovery seems quite high, and the future of the species in the area is promising. However, this population is small and still highly vulnerable to the potential impacts of varying human activities and behaviors, as reflected by the slower demographic response of the eastern subpopulation, compared to that of the western one. A direct comparison of the genomes of Cantabrian and Apennine bears, with the latter apparently less capable of demographic growth despite similar levels of protection, could possibly clarify the role of genetic load.

On the basis of the population trajectories and current status of the three European populations presented in this study, we believe that it is necessary to include more individual-based research (e.g. telemetry in the Cantabrian Mountains) in order to extend the available information essential for effective conservation and management, such as bear rhythms of activity, dispersal, home range behavior, and high-resolution space use. Additionally, more monitoring and conservation efforts should be accorded to dispersing bears (Maiorano et al. 2017), especially in the case of females or family groups detected outside the core range. Indeed, the identification, management, and conservation of critical corridors that may allow range expansion and connectivity among core habitats should be particularly focused on the biologically most important segments of bear populations, that is, females and juveniles (Balbontín et al. 2005; Maiorano et al. 2017; Morini et al. 2017).

The future of each one of these three small populations will also depend on the cooperation and management of local administrations, irrespective of which administration has primary jurisdiction at a local scale. Specific regulations and agency responsibilities may change, but bears will require trans-regional coordination in conservation and management policies (Penteriani et al. 2018b). Knowing the areas into which these populations are likely to expand would allow authorities and conservation organizations to focus information campaigns and pre-emptive/proactive damage control actions in these areas. Such proactive approaches are important for successful large carnivore conservation and management (Ripple & Beschta 2012). In addition, as brown bears disappeared from certain areas decades ago, local communities are no longer familiar with them. Thus, local information campaigns directed at both residents and other users, e.g. hunters and tourists, of areas of potential bear expansion represent a crucial strategy to reduce human–bear conflicts and promote coexistence.

Finally, it is worthwhile to note here that, especially in the case of small, isolated, and/or endangered animal populations, the effects of climate change on trophic resources may considerably override conservation and management efforts performed at other levels, e.g. reduction of human–wildlife conflicts, threat of anthropogenic footprints and activities, poaching, and habitat fragmentation. Thus, conservation plans for species at higher trophic levels, such as brown bears, should take into account climate change vulnerability assessments of those plant communities that represent primary food resources and shelter for the target species (Penteriani et al. 2019). Thus, together with conservation actions aimed at maintaining bears in their historical and current ranges, we encourage conservation and management practices targeted at those areas potentially favorable to habitation by bears during the recovery process, taking into account the current context of climate change.

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