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Evidence of a large carnivore population recovery: Counting bears in Greece

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ABSTRACT

Reliable population and density estimates are the cornerstone of effective conservation and management planning, as conservation priorities often arise in relation to population numbers. Despite increased public interest and costly conservation programs limited information on brown bear (*Ursus arctos*, Linnaeus, 1758) abundance and density in Greece exists. We carried out systematic non-invasive genetic sampling using hair traps on power poles, as part of a capture-mark-recapture study design in order to rigorously estimate abundance and density of the Pindos bear population in Greece. From 2007–2010 we identified 211 and estimated a mean of 182.3 individuals in four sampling areas; bear densities ranged from 10.0 to 54 bears/1000 km^2. These results indicate an important population recovery of this large carnivore in Greece in recent years; a conservative population estimate would place the population size in the entire country >450 individuals. Considering the results of the study and the increased negative interactions between humans and bears recorded currently in Greece, we suggest that systematic genetic monitoring using power poles should continue in order to collect the necessary information that will enable the definition of an effective Action Plan for the long-term conservation of this species.

1. Introduction

The brown bear (*Ursus arctos*) is a charismatic key species of the biodiversity of the Holarctic region (Servheen, Herrero, & Peyton, 1999), capable of attracting attention and resources to conservation efforts through its function as an iconic flagship species (Simberloff, 1999). Once, extirpated and threatened by extinction throughout large parts of Europe (Zedrosser, Dahle, Swenson, & Gerstl, 2001), bears have made a remarkable recovery, with populations increasing and expanding in several countries (Deinet et al., 2013). The benefits for nature conservation notwithstanding, such recoveries create the potential of increased human–wildlife conflicts and wildlife mortality (Gardner, Royle, Wegan, Rainbolt, & Curtis, 2010; Knott et al., 2014). In this context, informed, science-based management and conservation actions are urgently required to safeguard the recovery and survival of small bear populations; a task that has been identified as an important European conservation priority (Habitat Directive 92/43/CEE).

Brown bears in Greece reach their southern-most distribution in Europe and are therefore an important component of European biodiversity. They belong to the Dinaric–Pindos (DP) bear population, which has been identified as one of the largest and most important on the European continent (Zedrosser et al., 2001); the DP bear population appears to be stable, numbering more than 3000 individuals (Kaczensky et al., 2013). In Greece; however, bears are still considered to be endangered (Mertzanis, Giannakopoulos, & Pylidis, 2009). In recent years, numerous extra-limital appearances throughout the country (Karamanlidis, Krambokoukis, & Kantiros, 2008), and the increase in bear encounters with humans (Karamanlidis et al., 2012a; Karamanlidis, Sanopoulos, Georgiadis, & Zedrosser, 2011) suggest that the bear population in Greece might now be recovering (Mertzanis et al., 2009; Tsaparis, Karaiskou, Mertzanis, & Triantafyllidis, 2014).

Despite increased public interest and costly conservation programs, little information on abundance and density of bears in Greece exist. Bears are crepuscular and nocturnal, have large home ranges, and occur usually in low densities in rugged and forested terrain. Counting them by traditional field methods (e.g., direct

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observations, extrapolations of counts of mother with cubs of the year) might therefore be unreliable, expensive or sometimes even unfeasible (Mace, Minta, Manley, & Aune, 1994). Considering these difficulties, the current population estimate for bears in Greece, which is likely a combination of expert knowledge and observation counts (Mertzanis et al., 2009), might not accurately reflect actual population processes (Nichols & Williams, 2006). The current lack of information on the abundance of bears in Greece however, sharply contradicts the need to evaluate management and conservation actions carried out so far and develop a long-term and effective management and conservation strategy for the species (Ciucci & Boitani, 2008; Mertzanis et al., 2009).

Genetic methods play a pivotal role in bear conservation and cannot be neglected when developing effective conservation strategies and planning the long-term survival of threatened bear populations (Swenson, Taberlet, & Bellemain, 2011). One of the most attractive applications of genetic methods, commonly used now by management agencies (McCall et al., 2013) because it is considered more effective than traditional field methods (Garshelis, 2006), is the possibility of estimating the number of free-ranging individuals (Kohn et al., 1999). Coupled with non-invasive genetic sampling (NGS), which is ideal for studying endangered populations, as it precludes the unnecessary capture of individuals, and capture-mark-recapture (CMR) methods, genetic studies have been successfully deployed to obtain bear abundance and density estimates for large (McCall et al., 2013) and small study areas, with irregular sampling designs and small population sizes [i.e., <100 individuals (Gardner, Royle, & Wegan, 2009; Gervasi, Ciucci, Boulanger, Randi, & Boitani, 2012; Latham, Stetz, Seryodkin, Miquelle, & Gibeau, 2012; Obbard, Howe, & Kyle, 2010)].

The goal of this study was to apply non-invasive genetic sampling as part of a CMR study design in order to rigorously estimate bear abundance and density in Greece. Based on our results we identify research and management priorities for the effective conservation of *U. arctos* in the country.

1.1. Study area

Brown bears in Greece occur in two separate populations in the Pindos Mountains in the western and in the Rodopi Mountains in the eastern part of the country (Fig. 1A); the Pindos bear population is stable or locally increasing and is estimated to number approximately 190–230 individuals (Mertzanis et al., 2009). The study was carried out in the approximately 250 km-long Pindos mountain range (Fig. 1B). The study area forms a mosaic of elevations and habitats; elevations range from a couple of hundred meters above sea level (a.s.l.) up to the peak of Mount Smolikas at 2637 m a.s.l. Intensity of human activity ranges from areas with low human presence to major cities with populations >50000.

2. Methods

Genetic sampling was based on the ubiquitous marking and rubbing behaviour of bears (Green & Mattson, 2003) on wooden poles of the telephone and electricity network (hereafter power poles) in Greece (Karamanlidis, Youlatos, Sgardelis, & Scouras, 2007). In the preparatory phase of the study (2002–2006) we inspected and evaluated the suitability of 4147 power poles as non-invasive genetic sampling stations according to predefined criteria (Karamanlidis, 2008); then we conducted a pilot study that confirmed the suitability of power poles for the non-invasive genetic monitoring of brown bears (Karamanlidis et al., 2010).

For this study we selected 171 of the most suitable power poles and placed barbed-wire hair traps (Kendall & McKelvey, 2008) on them, thus creating four sampling areas [i.e., Vitsi–Varnoundas (VV), and Northern (NP), Central (CP) and Southern Pindos (SP) (Fig. 1C, Table 1)]. We selected location and size of the sampling areas so as to cover the maximum of the core range of brown bears in the Pindos mountain range; sampling areas were separated either by distance or/and geo-morphological features and human infrastructure. Sampling areas were established only within the core range of brown bears because of the difficulty to count bears in the periphery of the range of expanding brown bear populations (Swenson, Sandegren, & Soderberg, 1998). We calculated the size of the sampling areas by drawing a buffer zone of 5.86 km around the minimum convex polygon (MCP) defined by the outermost sampling stations in each study area; 5.86 km was the mean distance between all the individual bear recaptures recorded during the study. We carried out systematic sampling efforts in all four sampling areas during three 12-month sampling sessions (i.e., October 2007–September 2010), when poles were inspected and hair samples were collected monthly.

Each tuft of hairs on a set of barbs was considered a sample; hair samples were collected without contact to human skin, were placed in uniquely numbered paper envelopes labelled with the location and date of collection and then stored at room temperature in zip-lock bags with silica gel (Roon, Waits, & Kendall, 2003) until being analysed by Wildlife Genetics International (Nelson, British Columbia, Canada). DNA was extracted using the DNeasy blood & tissue kits (QIAGEN, Hilden, Germany), following the manufacturer's instructions. We did not attempt to extract DNA from hair samples with no guard hair or <5 underfur hairs.

To determine individual identity each sample was genotyped at the microsatellite loci G1D, G10J, G10L (Paetkau, Shields, & Strobeck, 1998; Paetkau & Strobeck, 1994), G10C, G10P (Paetkau, Calvert, Stirling, & Strobeck, 1995), MU51 and MU59 (Taberlet et al., 1997). Gender identification was established through the analysis of the amelogenin gene (Ennis & Gallagher, 1994). Up to 10 additional loci were analysed for ≥1 sample from each individual to enable more detailed population genetic analyses. These extended genotypes were used to confirm differences between individuals with similar 7-locus genotypes.

Thermal cycling was performed using a MJ Research PTC100 thermocycler with 96 well 'gold' blocks (MJ Research Inc., St. Bruno, Quebec, Canada). Polymerase chain reaction (PCR) buffers and conditions were used according to Paetkau et al. (1998), except that markers were not co-amplified, because co-amplification may reduce the success rates for hair samples (D. Paetkau, Wildlife Genetics International, pers. Comm., 2008). Two mM MgCl2 was used for all markers except G10J (1.8 mM). An automated sequencer (ABI 310) was used, and genotypes were determined using ABI Genescan and Genotyper version 2.1 software (PerkinElmer-Applied Biosystems, Foster City, California, USA). The sizing of the PCR products was performed using capillary electrophoresis.

Mixed samples (samples with hair from >1 bear) were reliably identified by evidence of ≥3 alleles at ≥1 locus (Roon, Thomas, Kendall, & Waits, 2005). To minimize genotyping errors in the final data set, low-quality and putatively mixed samples were excluded from further analyses (Paetkau, 2003). Genotypes were replicated for all: (1) individuals identified in one sample, (2) pairs of individuals that differed at only 1 or 2 loci (1- and 2-mismatch pairs) and (3) pairs of individuals that differed at 3 loci when ≥1 locus was consistent with allelic dropout. Tests for allelic dropout, presence of null alleles, and scoring errors caused by stutter peaks were performed with Micro-Checker version 2.2.3 (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). We used the observed number of alleles (A) and expected heterozygosity (H_e) to express genetic variation in our population. We calculated the probability of identity (P_{ID}) and of siblings (P_{SIB}) to describe the power of our markers to identify individuals (Waits, Luikart, & Taberlet, 2001) using the software GIMLET version 1.3.2 (Valière, 2002). To allow for the possibility

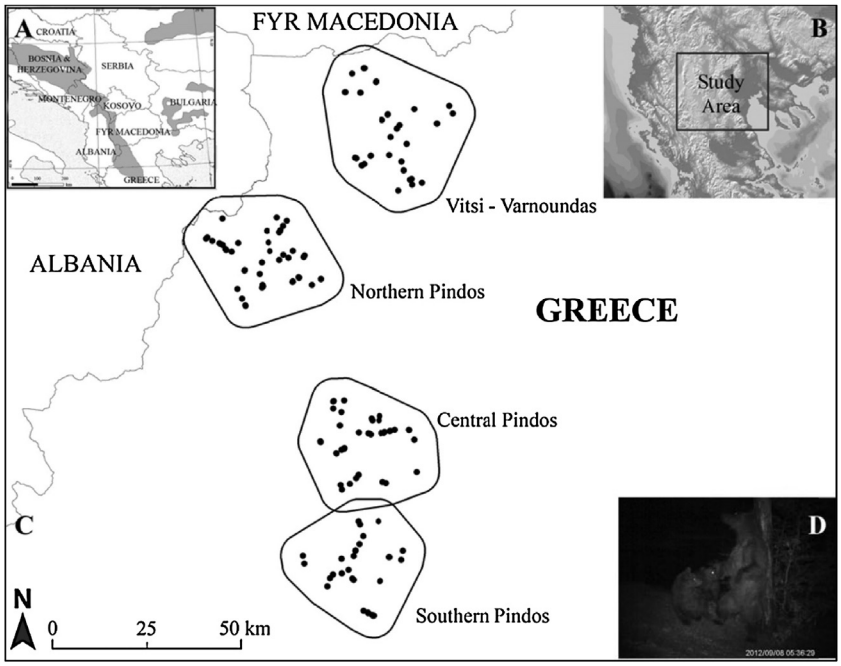

Fig. 1. (A) Map of south eastern Europe. The shaded areas indicate the approximate geographic range of brown bears in the region. (B) Geophysical map of Greece indicating the location of the study area. (C) Map of Greece indicating the location of four sampling areas for the non-invasive collection of genetic samples (2007–2010). (D) The inset photograph shows an adult female brown bear with her cubs rubbing on a power pole.

Table 1
Summary information of four sampling areas for the non-invasive collection of genetic samples from brown bears in Greece (2007–2010).

Sampling area	Location	Sampling area size (km^2)	Sampling stations (*N*)	Inter-pole distance (km)
Vitsi-Varnoundas	N: 40.6935, E: 21.3192	1270.39	40	15.25 ± 7.81
Northern Pindos	N: 40.3707, E: 21.0907	1066.22	45	13.20 ± 6.46
Central Pindos	N: 39.9197, E: 21.4054	999.72	47	12.52 ± 6.18
Southern Pindos	N: 39.6305, E: 21.3711	954.33	39	12.02 ± 6.14
Total		4290.66	171	13.20 ± 6.73

Table 2
Summary information of efforts at four sampling areas in Greece (2007–2010) for the non-invasive collection of brown bear hair samples.

Sampling area	Visits	Hair samples collected	Females identified	Males identified	Total *N* identified	*N* of animals recaptured	Mean distance between recaptures (km)
Vitsi-Varnoundas	1115	215	13	39	52	28	1.99 ± 2.64
Northern Pindos	1146	295	26	51	77	29	2.68 ± 3.45
Central Pindos	1220	249	19	42	61	33	2.27 ± 2.86
Southern Pindos	941	101	3	18	21	12	3.85 ± 3.34
Total	4422	860	61	150	211	102	2.51 ± 3.10

of mismatches caused by genotyping error, we also looked for the pairs of genotypes that were matched at all but 1, 2, and 3 loci (1-MM, 2-MM, and 3-MM pairs) using the program GenAlEx 6 (Peakall & Smouse, 2006).

To estimate population sizes, including dependent young, we used the Jolly–Seber (JS) CMR modelling framework that allows accounting for detectability less than one and dealing with open populations, i.e., systems in which births and deaths occur (Jolly, 1965; Seber, 1965). JS models provide estimates of abundance, probabilities of survival, detection and recruitment (sensu Schwarz & Arnason, 1996) i.e., the probability that an animal from the hypothetical super-population would enter the population on a particular time interval. We analyzed each of the four regions separately and obtained estimates of the female, male and total population sizes. We considered time and sex effects as possibly explaining environmental and individual variation in these demographic rates, entering in an additive or interactive way in the model, which led to a total of 125 candidate models. To select among these models, we used the Akaike's information criterion corrected for small sample size (AICc) (Burnham & Anderson, 2002) and used changes in AICc values (ΔAICc) to compare model support with reference to the model best supported by the data. To properly account for model uncertainty, annual abundance estimates were obtained by model averaging in which each model contributed to the final estimate according to its AICc weight (Burnham & Anderson, 2002). The analyses were performed using POPAN (Arnason & Schwarz, 1995) available in MARK (White & Burnham, 1999) that was called from R (R Development Core Team, 2011) with package RMark (Laake & Rexstad, 2008).

We tested the validity of important assumptions underlying the safe use of the JS model, such as the presence of transient individuals or an effect of trapping, using standard goodness-of-fit tests (Pradel, Gimenez, & Lebreton, 2005) as implemented in program U-CARE (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009). Although, we considered a potential effect of sex on the detection probability, other sources of individual heterogeneity might had

gone undetected in the present analysis, which could have led to severe bias in abundance estimates (e.g., Cubaynes et al., 2010). This for example could have been the case with individuals that were more active than others at the proximity of power poles, hence making them more capturable. To assess whether some individual heterogeneity was present besides gender effects, we compared for each of the four study areas the model best supported by the data to its counterpart, incorporating heterogeneity in the detection probability. To do so, we considered finite-mixture JS models (Pledger, Pollock, & Norris, 2010) that extend standard JS models by assuming that the animals come from different classes of detection, although we do not know which class each individual is from. Heterogeneous JS models were fitted using the R package 'hetage' that is available from http://homepages.ecs.vuw.ac.nz/~shirley/. To compare homogeneous and heterogeneous models, we resorted to a likelihood ratio test that was distributed under the null hypothesis of homogeneous detection probabilities as a 50:50 mixture of chi-square distributions with 0 and 1 degrees of freedom (Self & Liang, 1987; Gimenez & Choquet, 2010). Note that, to get the *P*-value of this test, using the mixture corresponds to halving the *P*-value from using the standard chi-square distribution with 1 degree of freedom.

We calculated bear density by dividing the mean population estimate over the three sampling years with the size of each sampling area respectively (Table 1). Less than 3% of the study areas were not suitable habitat for bears (e.g., lakes, rivers and human settlements); therefore we retained these areas in the sampled area and density calculations.

3. Results

3.1. Sampling effort

From 2007–2010, we conducted 4422 inspections to the 171 sampling sites and collected 860 hair samples (Table 2). We collected bear hair at 92.25% of all traps (i.e., VV: 95%; NP: 100%; CP: 95%; SP: 79%) during 25.75% of all inspections (i.e., VV: 30%; NP: 34%; CP: 26%; SP: 13%).

3.2. Genotypic success, marker power, and quality control

Of the 860 samples, we excluded 250 (29%) from the analysis due to insufficient genetic material (i.e., hair without follicles). Of the 610 samples that we attempted to analyze, 11 (1.8%) appeared to contain DNA from >1 individual, and 154 samples (25%) failed the DNA extraction process. From the remaining 445 samples (64% of total collected) 211 individuals were identified (61F, 151 M), from which 102 individuals were recaptured ≥2 times (Table 2). From the 211 individuals identified, 206 individuals (98%) produced complete 7-locus genotypes plus gender assignment.

Mean observed heterozygosity across the 7 markers used to identify individuals was 0.70 (Table 3). The probability that 2 randomly drawn, unrelated individuals would share the same genotype (P_{ID}) was 0.0000005, and the probability that full siblings would have identical genotypes (P_{SIB}) was 0.002 (Table 3). Based on the observed distribution of genotype similarity for the 7 loci used for individual identifications, we predicted that no pair of matching genotypes could exist within our dataset. Of the 211 individuals present in our analysis, 91% had ≥10-locus genotypes and, when all available loci were considered, all individual bears differed at ≥3 loci.

3.3. Abundance and density estimation

The standard assumptions of the JS model were valid as showed by the goodness-of-fit tests that were non-significant for all regions (VV $\chi^2_3 = 2.45$, p-value = 0.49; NP $\chi^2_4 = 3.58$, p-value = 0.47; CP $\chi^2_7 = 0.47$, p-value = 0.99; SP $\chi^2_2 = 0.71$, p-value = 0.70). Model selection showed contrasted effects between regions (Table 4). There was substantial uncertainty regarding the best model to

Table 3
Variability of microsatellite markers used to determine individual identity of brown bears in Greece, 2007–2010.

Marker	H_E[a]	H_O	A	P_{ID}	P_{SIB}
G1D	0.78	0.80	6	0.08	0.37
MU59	0.78	0.76	8	0.07	0.38
G10C	0.76	0.76	6	0.09	0.39
G10P	0.75	0.67	9	0.10	0.40
G10J	0.70	0.77	6	0.14	0.43
G10L	0.57	0.55	5	0.23	0.52
MU51	0.55	0.57	5	0.24	0.53
$\bar{x}$	0.70	0.70	6.42		
Overall probability of identity				5.299e-07	0.002

[a] H_E = expected heterozygosity; H_O = observed heterozygosity; A = number of alleles; P_{ID} = probability of identity; P_{SIB} = probability of identity among siblings.

Table 4
Model selection results from CMR analysis of brown bear populations in Greece using the Jolly–Seber modelling framework. For each of the four sampling areas, the Akaike's information criterion value corrected for small sample sizes (AICc), the difference in AICc value between the *i*th model and the model with the lowest AICc value (ΔAICc) are presented. The models best supported by the data had ΔAICc < 2. Constant (.), sex (s) and time (*t*) effects were considered on survival (ϕ), detection (p) and entry (b) probabilities either as main effect, in an additive (+) or in interactive (×) fashion. For each of the four regions, only the 10 top ranked models are displayed although 125 models were originally fitted to the data.

Sampling area	Model	k	AICc	ΔAICc
Vitsi-Varnoundas	ϕ(.) p(s) b(.)	5	95.17	0.00
	ϕ(s + t) p(.)b(s)	7	96.49	1.34
	ϕ(s) p(.) b(s)	6	97.51	2.36
	ϕ(t) p(s) b(.)	6	97.51	2.37
	ϕ(.) p(s) b(s)	6	97.54	2.39
	ϕ(.) p(s) b(t)	6	97.57	2.42
	ϕ(s) p(s) b(.)	6	97.58	2.43
	ϕ(s) p(.) b(.)	5	97.91	2.76
	ϕ(s + t) p(.)b(.)	6	98.26	3.12
	ϕ(.) p(.) b(s)	5	98.37	3.22
Northern Pindos	ϕ(s + t) p(.) b(s + t)	7	126.03	0.00
	ϕ(s) p(.) b(s + t)	8	126.19	0.16
	ϕ(s + t) p(s) b(s + t)	8	127.97	1.94
	ϕ(s) p(t) b(s + t)	11	128.02	2.00
	ϕ(s) p(s) b(s + t)	10	128.47	2.48
	ϕ(s + t) p(.) b(t)	11	128.67	2.64
	ϕ(s) p(.) b(t)	8	128.82	2.79
	ϕ(s) p(t) b(t)	9	129.09	3.06
	ϕ(s) p(t) b(s)	9	129.41	3.38
	ϕ(s + t) p(t) b(s + t)	9	129.95	3.92
Central Pindos	ϕ(s) p(.) b(.)	8	143.03	0.00
	ϕ(s) p(.) b(t)	8	143.64	0.61
	ϕ(.) p(s) b(.)	9	143.77	0.74
	ϕ(s + t) p(.) b(.)	7	144.56	1.54
	ϕ(.) p(.) b(.)	10	144.73	1.71
	ϕ(s) p(.) b(s)	9	144.75	1.72
	ϕ(s + t) p(.) b(t)	7	144.76	1.73
	ϕ(s) p(.) b(s + t)	10	144.82	1.79
	ϕ(.) p(s) b(t)	8	144.82	1.79
	ϕ(s) p(s) b(.)	11	144.83	1.80
Southern Pindos	ϕ(.) p(.) b(.)	4	55.05	0.00
	ϕ(s) p(.) b(.)	5	55.14	0.09
	ϕ(.) p(s) b(.)	6	57.84	2.78
	ϕ(t) p(.) b(.)	7	57.96	2.91
	ϕ(.) p(.) b(s)	5	57.98	2.93
	ϕ(s) p(s) b(.)	6	58.00	2.95
	ϕ(.) p(.) b(t)	6	58.04	2.99
	ϕ(s + t) p(.) b(.)	5	58.28	3.23
	ϕ(s) p(.) b(s)	8	58.39	3.34
	ϕ(s) p(.) b(t)	6	58.41	3.36

Table 5
Abundance estimates from CMR analysis of brown bear populations in Greece using the JS modelling framework. For each of the four sampling areas the time and sex-specific population size estimate, as well as the lower (LCL) and upper (UCL) confidence limits of the 95% confidence interval obtained from model averaging are presented.

Sampling area	Sex	Estimate	2007–8	2008–9	2009–10
Vitsi-Varnoundas	Female	Value	18.7	22.4	21.4
		LCL	4.9	7.1	5.2
		UCL	71.1	70.8	88.3
	Male	Value	43.0	47.4	50.8
		LCL	12.4	15.1	15.6
		UCL	148.7	148.6	165.2
	Pooled	Value	61.7	69.8	72.2
		LCL	19.7	24.7	23.6
		UCL	193.0	197.6	220.6
Northern Pindos	Female	Value	16.9	19.7	4.0
		LCL	8.7	10.1	0.7
		UCL	32.8	38.5	24.5
	Male	Value	44.9	46.5	27.7
		LCL	20.6	26.7	9.1
		UCL	97.7	81.3	84.6
	Pooled	Value	61.8	66.3	31.8
		LCL	31.1	38.7	9.9
		UCL	122.8	113.6	102.1
Central Pindos	Female	Value	22.2	14.5	11.4
		LCL	12.3	6.5	3.5
		UCL	40.1	32.4	37.2
	Male	Value	41.9	34.2	28.7
		LCL	26.4	21.2	13.9
		UCL	66.6	55.0	58.9
	Pooled	Value	64.1	48.6	40.1
		LCL	39.1	28.9	18.1
		UCL	105.0	81.9	88.6
Southern Pindos	Female	Value	2.1	1.0	0.9
		LCL	0.7	0.2	0.2
		UCL	6.0	4.8	3.8
	Male	Value	11.6	8.2	7.0
		LCL	7.6	5.4	3.8
		UCL	17.5	12.7	12.1
	Pooled	Value	13.6	9.3	7.7
		LCL	8.3	5.5	4.1
		UCL	22.3	15.6	14.4

select for all regions, with several models within the range ΔAICc < 2. Survival was sex-specific in all regions, with the addition of time except for SP, or constant in all regions but NP. Recruitment showed the most contrasted responses across regions. It was constant or sex-specific for VV, sex-specific with the addition of time for NP, constant, sex-specific or/and time-specific for CP and constant for SP. Detection was constant or sex-specific in all regions except for SP in which it was constant. We did not detect extra heterogeneity in the detection probability (VV $\chi^2_1 = 2.5$, p-value = 0.06; NP $\chi^2_4 = 2.6$, p-value = 0.31; CP $\chi^2_7 = 8.5$, p-value = 0.15; SP $\chi^2_1 = 0.6$, p-value = 0.22).

The most abundant region was VV with 68 individuals on average over the study period, followed by NP with 53 individuals, CP with 51 individuals and SP with 10 individuals (Table 5). The mean number of individuals estimated for all four sampling areas per year was 182.3 individuals.

Using the average population estimates over the three sampling years produced the following density estimates: VV: 54 bears/1000 km^2; NP: 50 bears/1000 km^2; CP: 51 bears/1000 km^2; SP: 10 bears/1000 km^2. Bear density, as expressed by the number of bears per 1000 km^2 and as the average number of unique bears identified per hair trap per cell (Fig. 2) was similar in the three northern sampling areas and decreased sharply moving towards the edge of the core range of the species in the Southern Pindos sampling area.

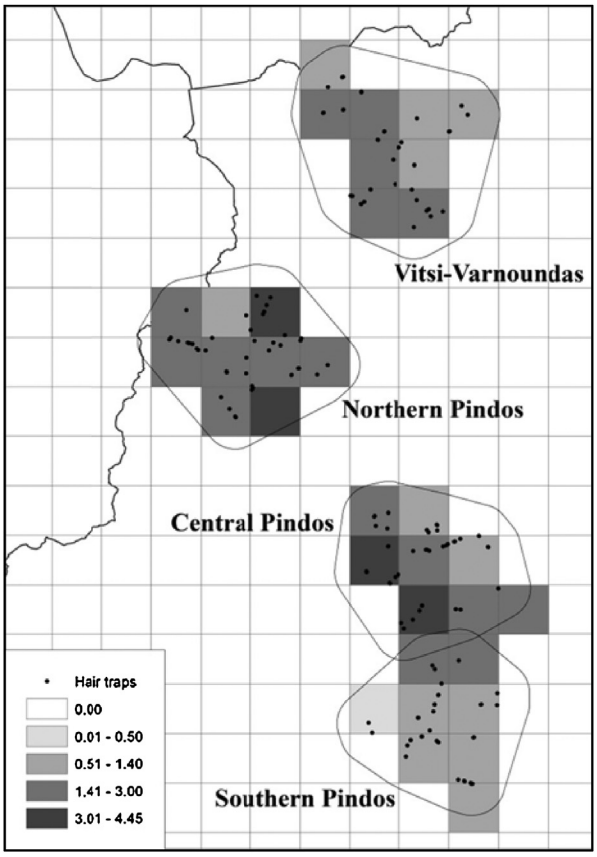

Fig. 2. Relative densities (i.e., unique bears identified per sampling station per UTM cell (10 × 10 km) of bears in four sampling areas in north western Greece (2007–2010).

4. Discussion

We present the first rigorous, systematic and large-scale effort to estimate abundance and density of the Pindos bear population in Greece. The study was carried out in four sampling areas covering the core range of the Pindos bear population. By using genetic data from hair samples collected exclusively from power poles, an approach that has not been implemented in this scale before, and using a CMR modelling approach, we obtained precise and unbiased population estimates despite fairly low capture and recapture rates.

There are several assumptions that need to be checked in order to use the JS modelling framework and obtain reliable abundance estimates. First, we assumed that there was no immigration or emigration (i.e., closure assumption) between the four regions we studied. This was true as only one individual moved from SP to NP during the study period. A modelling option would have been to use multisite JS models (e.g., Lebreton, Nichols, Barker, Pradel, & Spendelow, 2009) instead of considering the region as a factor, hence allowing the estimation of movement between regions. However, with so few individuals actually making the transitions between regions, fitting multisite JS models would be numerically unstable with movement parameters estimated on the boundary (Gimenez et al., 2005) and identifiability issues (Gimenez, Choquet, & Lebreton, 2003). A second assumption underlying the application of JS models is that all animals, marked or unmarked, should have the same capturability (i.e., homogeneous capturability assumption). Here, there was no reason to believe that the use of poles to "capture" individuals would distinguish between marked and unmarked individuals. Third, the duration of the sampling period

should be short in comparison to the time between sampling occasions. In our study, most of the detections were made over eight months, which was considered short enough with regard to the yearly time interval we used between sampling periods, as bear survival was high (Hargrove & Borland, 1994). Fourth, and probably the most crucial assumption, detection probabilities were assumed homogeneous between individuals while heterogeneity, if present and ignored, is a source of strong bias in the abundance estimates (Cubaynes et al., 2010). We found a sex effect for all populations but SP, and this difference was accounted for when calculating (model-averaged) abundance estimates. For example, in the VV population males were more detectable than females [0.18 (SE = 0.12) for females and 0.38 (SE = 0.08) for males]. Increased male detectability has been encountered also in other non-invasive genetic studies using poles and rub trees (Karamanlidis et al., 2012b; Kendall et al., 2009). We also tested for extra individual heterogeneity not explained by differences between males and females, but did not find any, which suggests that the risk of bias in abundance estimates was avoided. Last but not least, it is usually assumed that individuals retain their mark throughout the study and that these marks are read correctly. When interpreted in the context of DNA marking, these two assumptions refer to data quality and the possibility of genotyping error. The laboratory protocols followed and the marker power and quality control data indicate that it is unlikely that an individual was misidentified in our study.

Our sampling, genetic analysis and modelling efforts resulted in precise density and abundance estimates for the Pindos bear population. Although, bear density is an important parameter in the design of effective management and conservation plans it should be used with caution in comparisons with other populations due to innate differences in the studies they originate from (Kendall et al., 2008). Bear densities obtained in the four sampling areas in Greece were the lowest recorded for the species in the Dinara–Pindos population [i.e., see Slovenia (Jerina, Jonozovič, Krofel, & Skrbinšek, 2013) and Croatia (Huber et al., 2008)]. This is consistent with the assumption of a Dinara–Pindos population with a core population in the North and expanding towards the South (Kaczensky et al., 2013). It should be noted however, that both aforementioned countries have different management regimes for bears (i.e., supplemental feeding is supported) and therefore higher bear densities should be expected. Furthermore, bear densities in the three northern sampling areas in Pindos were comparable to the upper limits of bear densities in Sweden, a country which is considered to host a bear population with a favourable conservation status (Soldberg, Bellemain, Drageset, Taberlet, & Swenson, 2006; Zedrosser, Pelletier, Bischof, Festa-Bianchet, & Swenson, 2013). They were also comparable to several healthy bear populations in North America (Mowat et al., 2005; Romain-Bondi et al., 2004) and considerably higher than the density of the highly endangered bear population in the Abruzzo region in Central Italy (Lorenzini & Posillico, 2000). Only SP had a bear density that was comparable with that of Abruzzo; the low number of female and the high number of male bears identified (Table 2) and estimated (Table 5) in SP are consistent with the assumption of the area being at the edge of the core range of the species in the country (Krofel, Filacorda, & Jerina, 2010; Swenson et al., 1998). It is also consistent with the high number of human-bear conflicts in the area (Karamanlidis et al., 2011), which are usually attributed to male bears (Benn & Herrero, 2002). Overall, relative bear densities matched expectations based on knowledge of the distribution of the species in the region (Bonnet-Lebrun, Karamanlidis, De Gabriel Hernando, & Gimenez, 2014) and gene flow between the two genetically distinct bear populations in the region (i.e., VV vs. NP, CP and SP) (Karamanlidis, Unpublished data).

Reliable population estimates are the cornerstone of effective conservation and management planning, as conservation priorities often arise in relation to population numbers (Kendall et al., 2008); they have been carried out for several European bear populations (Huber et al., 2008; Lorenzini, Posillico, Lovari, & Petrella, 2004; Pérez et al., 2014; Skrbinšek et al., 2012). Our population estimates for VV and NP, and CP are comparable with previous short-term efforts to estimate bear abundance in the region (Karamanlidis et al., 2012b; Tsaparis et al., 2014). Overall, the mean number of bears estimated (i.e., 182.3 individuals) and the minimum number of individuals identified (i.e., 211 individuals) in all four sampling areas corresponds almost to the official, minimum population estimate for the entire Pindos population (Mertzanis et al., 2009), despite the fact that in the present study only approximately half the core range and one third of the entire range of the Pindos bear population were sampled. The differences in bear abundance between the present study and the official estimate are to a certain degree due to methodological differences: official estimates were based mainly on observations of females with cubs counts, a method that accurately captures the general population size but tends to underestimate the true population size (Soldberg et al., 2006).

We do not believe however, that methodological differences are entirely responsible for the differences in abundance estimates between the official population estimate for the Pindos bear population (Mertzanis et al., 2009) and the present study. Considering: (a) the abundance estimates of our study, (b) the fact that over a three-year monitoring period bear recaptures between study areas occurred only once, (c) the small size of the study area compared to the entire range of brown bears in the Pindos mountain range, (d) the increase of extralimital sightings in the region (including mothers with cubs) (Karamanlidis et al., 2008), and (e) the increase of bear encounters with humans (Karamanlidis et al., 2011), we believe that the Pindos bears population is currently at least twice the size than previously assumed. Adding to this estimate the estimate for the Rodopi bear population [and assuming that this has remained stable (Mertzanis et al., 2009)] we speculate that a conservative population estimate for the entire bear population in Greece is >450 individuals. This is indicative of a significant population recovery of the bear population in Greece in the past decade and is consistent with a recent study of large carnivore population recovery in Europe, including Greece (Chapron et al., 2014).

5. Conclusions and recommendations

Since the 1980s, several conservation efforts have been carried out for the protection of the brown bear in Greece. It is hard to evaluate how exactly these efforts have benefitted the species, but the recovery of the Pindos bear population is currently a fact that the Hellenic state has to acknowledge and deal with effectively. Our study provides the methodological background for monitoring bears in Greece, while the data presented in this study will be useful as benchmarks for monitoring future trends in the size, density and overall status of local bear populations in Greece. Based on our study we recommend the following research and conservation actions:

- Considering the limited logistic and financial means available to the Hellenic state for bear monitoring, we believe that the methodology developed in the present study is ideal for monitoring bears in Greece and should be used in future monitoring efforts in the country. Genetic monitoring is generally cheaper and more accurate than traditional fields methods (Soldberg et al., 2006), such as the ones applied so far in the monitoring of bears in the country. The methodology developed in the present study has taken genetic monitoring to the next step: the exclusive use of power poles resulted in lowering the logistic and financial

requirements for the effective monitoring even more. Compared to rub trees, power poles are easier to identify and do not require extensive prior knowledge of bear biology and habitat use. They are also easy to access making power poles easy to monitor. It is characteristic, that the present study used a single field biologist to carry out all the sampling efforts.

- Our study has produced bear abundance and density estimates for the Pindos bear population with a proper quantification of uncertainty. The precision of these estimates could be improved by the use of additional data sources (Gervasi et al., 2012), such as occupancy data (Blanc, Marboutin, Gatti, Zimmermann, & Gimenez, 2014).

Brown bears are a long-lived species; the collection of basic biological parameters requires a long-term commitment in the monitoring of the species. We believe that monitoring power poles is a unique tool for doing this in Greece. Not only does it provide the opportunity to collect data on the population status of the species, but also on the distribution (Bonnet-Lebrun et al., 2014; Karamanlidis et al., 2007), the genetic status (Karamanlidis, 2008; Karamanlidis et al., 2012b) and the behaviour of the species (Karamanlidis et al., 2007). All this information will be necessary in order to define an Action Plan for the species that will effectively mitigate the increasing negative human-bear interactions (Karamanlidis et al., 2011) and safeguard the long-term survival of the species in the country.

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