Dispersal patterns of a recovering brown bear (*Ursus arctos*) population in a human-dominated landscape

Alexandros A. Karamanlidis,*,#,® Alexander Kopatz,# and Miguel de Gabriel Hernando

ARCTUROS, Civil Society for the Protection and Management of Wildlife and the Natural Environment, Aetos, Florina, 53075, Greece (AAK, MdGH)
Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, 1432, Norway (AAK)
Norwegian Institute for Nature Research (NINA), Trondheim, 7485, Norway (AK)
Department of Biodiversity and Environmental Management, Faculty of Biological and Environmental Sciences, Universidad de León, León, 24007, Spain (MdGH)

*Correspondent: akaramanlidis@gmail.com
#These authors contributed equally to this study.

Despite increasing habitat fragmentation, large carnivore populations in parts of Europe have been recovering and expanding into human-dominated areas. Knowledge of animal dispersal patterns in such areas is important for their conservation, management, and coexistence with humans. We used genetic data based on 15 microsatellite markers from 312 individuals (98 females, 214 males) to assess kinship and dispersal patterns during the recovery and spatial expansion of a wild brown bear (*Ursus arctos*) population (2003–2010) in the human-dominated landscape of Greece. We hypothesized that bear dispersal in Greece was sex-biased, with females being more philopatric and males dispersing more frequently and over greater distances. Dispersal indeed was sex-biased, with males dispersing more frequently and farther than females. Overall, females were found to be philopatric; males also appeared to be philopatric, but to a lesser degree. However, a high proportion of females displayed dispersal behavior, which may be indicative of a pre-saturation stage of the population in that part of the country. Our results indicate that dispersal may be due to evading competition and avoiding inbreeding. We also documented long-distance dispersal of bears, which is considered to be indicative of a spatially expanding population. Our results highlight the value of using noninvasive genetic monitoring data to assess kinship among individuals and study dispersal patterns in human-dominated landscapes. Brown bears remain threatened in Greece; we therefore recommend systematic genetic monitoring of the species in combination with careful habitat management to protect suitable habitat (i.e., dispersal corridors) and ultimately ensure co-existence with humans and survival of brown bears in the country.

Key words: genetic relationship, Greece, kinship, spatial autocorrelation, wildlife conservation

Biodiversity is in decline worldwide and effective conservation measures are necessary for maintaining intact ecosystem processes and thereby securing human survival (Rands et al. 2010). One of the principal current and future threats to biodiversity is habitat fragmentation (Tilman et al. 2017). As ecosystems become more fragmented, populations become disconnected and effective dispersal increasingly challenging, but also very important because dispersal is the principal mechanism by which organisms expand as well as move among populations within a metapopulation structure. Dispersal maintains genetic connectivity, thereby increasing long-term population viability (Clobert et al. 2012). There accordingly has been increased interest in understanding the causes and mechanisms of dispersal, particularly across human-dominated, fragmented landscapes, often with a focus on improving interpopulation connectivity in threatened species (Braaker et al. 2017; Inoue and Berg 2017).

In terrestrial mammals, dispersal strategies are influenced by numerous ultimate and proximate causes (Bowler and Benton 2005), which in turn affect the fitness of entire populations, for instance by affecting extinction and colonization. Individual dispersal

propensity appears to be multifactorial, context-dependent, and highly individualistic (Cote et al. 2010). Sex-biased dispersal appears to be an almost ubiquitous feature of terrestrial mammals' life history (Lawson Handley and Perrin 2007) and is strongly influenced by a species' mating behavior (Greenwood 1980; Mabry et al. 2013). Dispersal patterns have evolved under a large variety of selective pressures and vary considerably in the mode of dispersal and in the proximate causes that have been invoked to explain them (Lawson Handley and Perrin 2007).

Brown bears (*Ursus arctos*) are solitary, nonterritorial carnivores with a promiscuous mating system (Bellemain et al. 2005). They are considered globally by the IUCN as species of Least Concern (McLellan et al. 2017) and are the only ursid in Europe. While a few, large, brown bear populations exist in Europe (e.g., Scandinavia, Karelia, Carpathian Mountains—Chapron et al. 2014), several small and isolated populations also persist that are threatened by habitat loss, fragmentation, and human–bear conflicts (Swenson and Sandegren 2000; Bautista et al. 2017; Piédallu et al. 2019). This is particularly the case in the southernmost European distribution of the brown bear in Greece, where the EU Habitats Directive requires designated management areas. The brown bear population in Greece is considered to be endangered, numbering fewer than 500 individuals (Karamanlidis et al. 2015b). Despite increasing human–wildlife conflicts (Karamanlidis et al. 2011), the bear population in the country has been recovering in recent years (after approximately the year 2000), both demographically (Karamanlidis et al. 2015b) and genetically, while previously isolated population fragments are in the process of reconnecting (Karamanlidis et al. 2018). At the same time, the species also has been expanding its range, with bears dispersing mainly into human-dominated landscapes, but also into areas with suitable habitat outside designated management areas. This recent recolonization has resulted in almost doubling the distribution range of brown bears in Greece, from approximately 13,500 km^2 to 30,200 km^2 (Bonnet Lebrun et al. 2019).

In general, functional dispersal is challenging to assess (Sutherland et al. 2000) and therefore still is poorly understood, particularly in human-dominated landscapes (Reinhardt et al. 2019). Understanding such dispersal patterns therefore is crucial for identifying priority conservation areas and for designing and implementing effective management measures that will promote the co-existence and recovery of the brown bear in Greece, as well as that of other large carnivores in human-dominated landscapes in general (Leidner and Haddad 2011; Driscoll et al. 2014).

Sex-biased dispersal appears to be the norm in ursids. It has been recorded in brown bears in Scandinavia (Zedrosser et al. 2007) and has been instrumental in population persistence of bears in Slovenia (Jerina and Adamic 2008). Also in accordance with theoretical models (Liberg and von Schantz 1985), female brown bears in general are more philopatric, while male bears are more likely to disperse across greater distances than females (Støen et al. 2006; Zedrosser et al. 2007).

We used genotype data to assess kinship and the dispersal patterns of brown bears in Greece during the period of their genetic and demographic recovery, as well as their range expansion. We hypothesized that male and female bears would exhibit different dispersal behavior, with females being more philopatric and males more likely to disperse from their natal sites and across greater distances.

MATERIALS AND METHODS

Study area and sampling methods.—The study was carried out throughout the western range of the brown bear in Greece (Karamanlidis et al. 2018) and extended over the approximately 250-km-long section of the Pindos mountain range (40°00′N, 21°03′E), reaching from the border of Albania and Northern Macedonia in the northwest, to central Greece (Fig. 1). Intensity of human activity in the study area ranges from areas with low human presence (16 inhabitants/km^2) to major cities with populations > 50,000; there is a relatively high density of smaller settlements in the region (6 settlements/100 km^2). This human activity has resulted in a mosaic landscape, where natural habitats are disrupted by agricultural patches. Human settlements in the study area are connected through an extensive road network (1.24 km/km^2). The construction and operation of two major highways in the study area in recent years has resulted in increased bear mortality from collisions with vehicles and has raised concerns about the effect of these highways on bear habitat connectivity and gene flow (Karamanlidis et al. 2012).

Sampling efforts were based mainly on a monthly noninvasive collection of hair samples from wooden poles of the electricity network that were not baited and were used by the bears as rubbing stations (Karamanlidis et al. 2010), following the study design described in Karamanlidis et al. (2012, 2015b). We complemented our hair sampling with tissue samples that were collected from road-killed animals.

Genetic analyses.—We used genetic data from 312 brown bears (98 females and 214 males) sampled during the period from 2003 to 2010 in western Greece, which were used in previous studies to assess the size and structure of the local bear population (Karamanlidis et al. 2015b, 2018). We also included in the study data from four individual bears that were identified close to the borders of Greece, in southern Albania (Karamanlidis et al. 2014a) and Northern Macedonia (Karamanlidis et al. 2014b). The laboratory procedures and protocols for DNA extraction, microsatellite analysis, error-checking, and quality assurance, have been previously described (Karamanlidis et al. 2012, 2015b, 2018). Each individual was genotyped at 18 microsatellite loci (for more information, see Supplementary Table SD1). Gender identification was established through the analysis of the amelogenin gene (Ennis and Gallagher 1994). PCR products were run in an automated sequencer (ABI 310) and genotypes determined using ABI Genescan and Genotyper version 2.1 software. Genotyping was carried out by Wildlife Genetics International (Nelson, British Columbia, Canada).

Genetic marker systems need to be evaluated when used to infer close relatedness or kinship among individuals, because errors may result in inaccurate and biased relationships
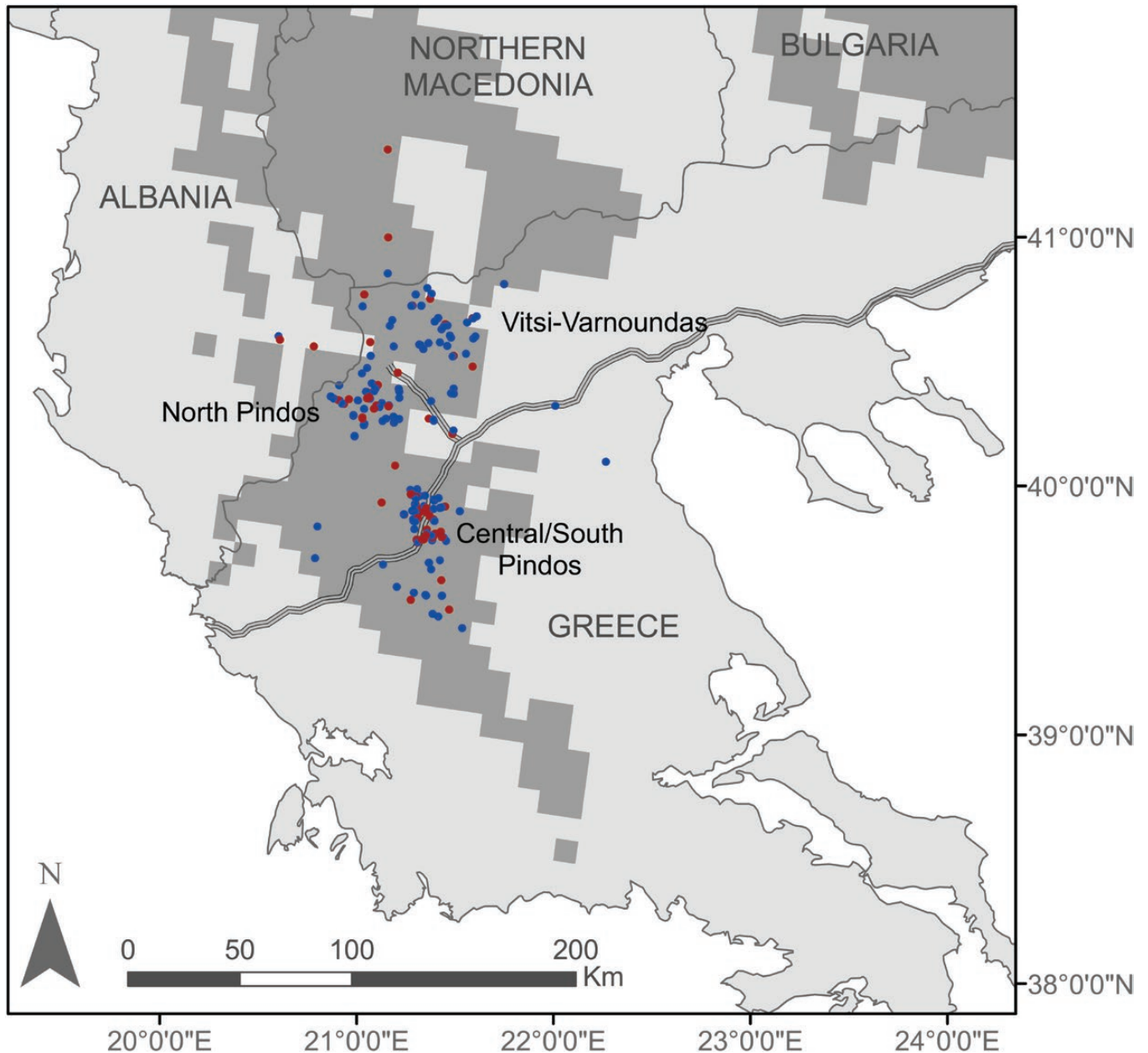
Fig. 1.—Map of a part of continental Greece, southern Albania, and southern Northern Macedonia indicating the location where 312 female (red) and male (blue) brown bears were sampled (2003–2010). Dark gray shaded areas indicate the approximate brown bear distribution in Greece, according to Chapron et al. (2014). The map indicates the general location of the three brown bear subpopulations in western Greece identified by Karamanlidis et al. (2018), and the two major highways in the study area.

(Pemberton et al. 1995; Selkoe and Toonen 2006). Thus, we evaluated the genotype data of our study based on successful genotyping and missing data, and calculated the matching, discrimination, and exclusion, probabilities (for more information, see Supplementary Materials). Fifteen of the 18 markers displayed a call rate of > 85%. Three markers (A06, M-sut2, MU26) had a call rate below this value and a large proportion of allele data missing. Based on our evaluation (i.e., combination of missing data and discrimination probability, deviations from Hardy–Weinberg equilibrium), these three markers were removed from the downstream analyses. Of the 312 genotyped samples from individual brown bears, 307 (98.3%) were hair

samples and five (1.6%) were tissue samples. Genotyping success was high, with 260 (88.4%) of the samples resulting in genotypes from all 15 remaining loci.

Genetic data were used to reconstruct kinship among bears in our study area. Kinship reconstruction focused on first-order relationships, i.e., parent–offspring and full-sibling relationships. We calculated the likelihood ratio (LR, i.e., which pair of relationships is more likely than the other) for all pairs of genotypes, using the program FAMILIAS 3.2.2 (Egeland et al. 2000; Kling et al. 2014). FAMILIAS distinguishes genealogical relationships without additional information, based only on genotype data and if putative

family members share zero, one, or two, alleles at a locus identical by descent (Blouin 2003). For our analyses we selected FAMILIAS because it is one of the few programs that has been validated to forensic genetic guidelines (Drábek 2008) and because it also has been successfully used of late to determine family relationships and dispersal in wildlife (Holmala et al. 2018).

Thresholds should be evaluated on the genetic marker set used to identify acceptable LR cutoff values with sufficient proof for a relationship in kinship analyses of wildlife and humans (e.g., Sulzer et al. 2011; Kopatz et al. 2017). We simulated 1,000,000 parent–offspring and full-sibling relationships in FAMILIAS to determine the suitable LR cutoff value to accept a relationship in our study, but also to keep the number of false negatives and positives at a minimum (Egeland et al. 2000; Sulzer et al. 2011). A previous study in the area (Karamanlidis et al. 2018) identified population substructure in the local bear population into three groups: Vitsi-Varnoundas, North Pindos, and Central/South Pindos. The average degree of differentiation was a pairwise $F_{ST} = 0.087$, which was used as a correction factor Θ during kinship reconstruction to account for potential effects of population substructure. Mutation rates of microsatellites in wildlife studies largely are unknown, particularly for the markers in our study (Ellegren 2004). We therefore ran the kinship analysis using mutation rates typically found in humans (Ruitberg et al. 2001), between 0, 0.1, and 0.2. As the mutation model, we assumed an equal mutation rate on all 15 markers.

Dispersal patterns.—Using the results from the kinship reconstruction and the first location where each individual was sampled, we calculated the pairwise (Euclidean) spatial distance between every pair of related bears to evaluate the frequency of effective dispersal (i.e., movement beyond an animals' home range), using the diameter of the average annual home ranges of adult females (8 km) and males (16 km) reported by De Gabriel Hernando et al. (2020) for bears in the study area. We then compared the effective dispersal frequency between the three possible sex combinations of relatives through a Pearson's chi-squared test and the dispersal distances between sex combinations using Kruskal–Wallis and post hoc Dunn tests. The same methodological approach was used to compare between type of relationship (i.e., parent–offspring versus siblings) within each sex combination (R statistical computing environment—R Core Team 2019). We also ran a spatial autocorrelation analysis to assess the relationship between spatial and genetic distance among all pairs of female and male bears by using GENALEX 6.5, with distance classes of 5 km and 9,999 permutations (Peakall and Smouse 2006, 2012). Because there has been population substructure reported (Karamanlidis et al. 2018), which may skew spatial autocorrelation (Peakall et al. 2003), we reran the analysis for the three bear subpopulations in western Greece.

RESULTS

The matching probability was low (0.07–0.228), while the discrimination probability was high (0.772–0.93). The exclusion

probability for each locus was comparably moderate, ranging from 0.249 to 0.593. However, the combination of all loci reached a cumulative exclusion probability of 0.9998 (Supplementary Table SD1).

Using a cutoff value of LR ≥ 20 in our simulations of true parent–offspring relationships yielded 98.7% of simulations that were equal to or above the LR limit (see Supplementary Table SD2). Simulating the alternative hypothesis yielded 0.19% false positives. Similarly, when simulating true full-sibling relationships, an LR ≥ 20 yielded 84.91% simulations that were equal to or above the LR limit. Simulating the alternative hypothesis yielded 0.36% false positives. Furthermore, an LR of 20 represented significant support (95% probability of relatedness) based on the a priori probability of 0.5 of the individual bears being related or unrelated (Marshall et al. 1998; Ayres 2000). Applying a higher LR cutoff value of LR ≥ 500 and LR ≥ 1,000 decreased the number of false positives to 0.01 – 0.03, but at the same time increased substantially (up to 46%) the number of false negatives (see Supplementary Table SD2). In addition, the application of higher cutoff values substantially reduced the number of relationship pairs that could be used as data for comparison in our study. We therefore chose a cutoff value of LR ≥ 20 as the lowest threshold to accept a relationship in our study.

Based on the cutoff value of LR ≥ 20, we identified 165 parent–offspring (Supplementary Table SD3) and 55 full-sibling relationship pairs (Supplementary Table SD4) when using a mutation rate of zero, and 189 parent–offspring and 111 full-sibling relationship pairs when using a mutation rate of 0.1 and 0.2. We adopted a conservative approach and carried out the analysis with the lower number of relationship pairs.

We identified 220 first-order relationships (38 female–female [28 parent–offspring and 10 full-siblings]; 99 male–male [73 parent–offspring and 26 full-siblings]; and 83 male–female [64 parent–offspring and 19 full-siblings]) among the 312 genotyped brown bears (see Supplementary Tables SD3 and SD4). Of these identified relationships, 149 (67.7%) included all 15 markers, and, due to missing data, 71 (32.3%) had 14 and less markers overlapping. Missing alleles were not considered as distinctive alleles. These relationships were plotted (Fig. 2) and their straight distances measured (Table 1).

Dispersal patterns.—Effective dispersal was more frequent (61.6%) for male–male relationship pairs than for male–female (51.8%) and female–female (39.5%) relationship pairs. These differences only had weak statistical support according to a Pearson's chi-squared test ($\chi^2 = 5.70$; $P = 0.058$). Differences in dispersal distances among sex combinations were significant ($\chi^2 = 39.31$; $P < 0.001$), with the highest average dispersal distances detected for male–male pairs (32.13 ± 22.76 km), followed by male–female (24.17 ± 22.84 km), and female–female pairs (11.46 ± 20.55 km) dispersal distances. The longest dispersal distances recorded were 103.89 km for a male–male and 118.55 km for a female–female relationship (Table 1). We did not detect significant differences in effective dispersal frequency, nor in dispersal distances between type of relationship (parent–offspring versus siblings) within each sex combination.
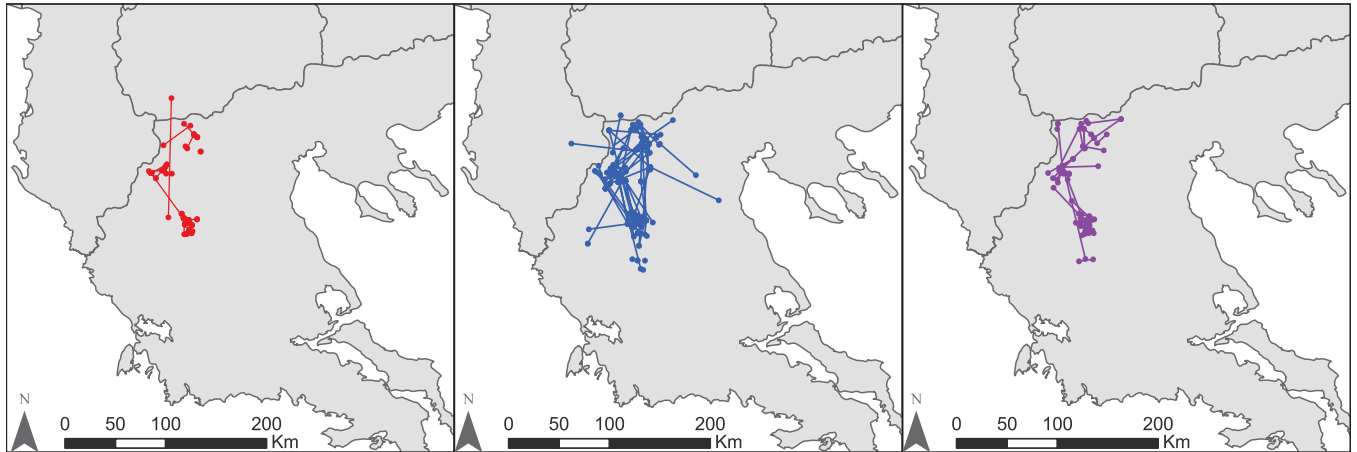
Fig. 2.—Map of the study area indicating the dispersal distance (i.e., based on the first location where each individual was sampled) between female (left, red), male (center, blue), and female–male (right, purple) full-sibling and parent–offspring of brown bears in Greece (2003–2010).

Table 1.—Dispersal distances (in km) between different sex combinations of relatives and relationships for brown bears in Greece (2003–2010).

Sex combination/relationship	n	Avg.	SD	Min.	Max.	Comparison	Z	P
Female–female	38	11.5	20.6	0.0	118.6	M–F	−4.166	< 0.001***
Parent–offspring	28	10.6	21.8	0.0	118.6			
Siblings	10	13.8	17.3	2.7	55.5			
Male–male	99	32.1	22.8	0.2	103.9	F–F	−6.261	< 0.001***
Parent–offspring	73	30.6	23.2	0.2	103.9			
Siblings	26	36.5	21.3	7.0	83.8			
Male–female	83	24.2	22.8	0.0	97.3	M–M	−2.545	0.011*
Parent–offspring	64	23.7	23.6	0.0	97.3			
Siblings	19	25.6	20.7	1.9	71.2			
Total	220	25.6	23.5	0.0	118.6			

n = Number, Avg. = Average, SD = Standard deviation, Min. = Minimum, Max. = Maximum. The significance levels are $P < 0.001$ (***) and $P < 0.05$ (*).

Female brown bears in Greece displayed a relationship of genetic relatedness and geographical distance until a distance class of 10 km (Fig. 3). Male brown bears in Greece showed a similar, albeit weaker, pattern of spatial autocorrelation, where related individuals were found more likely than unrelated ones until a distance class of 30 km. The slopes of females and males differed; however, this difference was not significant ($P = 0.327$). On a more local geographical scale, male brown bears did not display any pattern of spatial autocorrelation, while such a pattern was also not as pronounced for females compared to the overall, large-scale assessment (Fig. 4). More particularly our results indicated a weak pattern of spatial autocorrelation in females at a very close distance of 5 km in Vitsi-Varnoundas and Central/South Pindos. Sample sizes included in the analyses varied for each subpopulation: Vitsi-Varnoundas, males $N = 47$, females $N = 17$; North Pindos, males $N = 63$, females $N = 29$; Central/South Pindos, males $N = 89$, females $N = 39$.

DISCUSSION

The brown bear population in western Greece has been recovering recently, creating an urgency to understand the dispersal patterns of the species in a human-dominated landscape, thereby to implement effective management and conservation measures (Stoner et al. 2013). By assessing close kinship of the noninvasively sampled individuals we demonstrate that the dispersal behavior between female and male brown bears in Greece differed significantly. A pattern that would have remained obscure or undetected by the application of more general analyses, such as spatial autocorrelation.

Our analysis of related individuals showed that the overall dispersal of brown bears in Greece was sex-biased and males dispersed more frequently than females and over significantly greater distances. A similar sex-biased dispersal behavior has been recorded for brown bears in the United States (McLellan and Hovey 2001; Proctor et al. 2004), Finland (Kojola and Laitala 2000), Slovenia (Jerina and Adamic 2008), Romania (Fedorca et al. 2019), and Sweden, where male bears usually are the dispersing sex and females are philopatric and tend to stay close to their natal areas (Støen et al. 2006; Zedrosser et al. 2007). However, the relatively high percentage of female bears dispersing in Greece (39.5%) was in stark contrast to the strong female philopatry that has been reported from most of the stable North American brown bear populations (Glenn and Miller 1980; Blanchard and Knight 1991; McLellan and Hovey 2001). High percentages of dispersing females have been recorded only in the recovering and spatially expanding bear populations in Scandinavia and Finland (Swenson et al. 1998; Kojola et al. 2003, 2006). It has been hypothesized that

the high proportions of dispersing females might be due to the pre-saturation of a recovering population and the availability of unoccupied areas at the edges of the population (Støen et al. 2006).

Dispersal distances recorded in Greece were equal or greater than those recorded for the North American brown bear (McLellan and Hovey 2001; Proctor et al. 2004), but shorter than those recorded for brown bears in Scandinavia (Støen et al. 2006; Zedrosser et al. 2007). These observed differences may be due to variations in population densities between the different areas (Støen et al. 2006) and/or due to differences in average annual home range sizes (e.g., Greece [122.7 km^2] versus Scandinavia [397.1 km^2]—De Gabriel Hernando et al. 2020 versus Dahle and Swenson 2003). With respect to the dispersal

Fig. 3.—Spatial autocorrelation of female (red) and male (blue) brown bears in Greece (2003–2010) based on 15 microsatellite markers. The y-axis represents the genetic correlation coefficient (*r*) and the x-axis the 5-km distance classes. The dotted line shows the 95% confidence interval for the null hypothesis of random distribution of genotypes.

direction, information from spatially explicit models (Wiegand et al. 2004) and from other expanding bear populations (Kojola et al. 2003), in combination with information from gene flow (Karamanlidis et al. 2018) and range expansion of brown bears in Greece (Bonnet Lebrun et al. 2019), would suggest that more individuals dispersed from the central parts of Greece into the outermost edges of the population.

The long-distance dispersal (118.55 km) recorded in our study for a single female bear in Greece is not uncommon. As with the high percentage of dispersing females, long-distance dispersal also is considered to be a characteristic of recovering and spatially expanding bear populations and also has been documented in Scandinavia (Swenson et al. 1998), Slovenia (Jerina and Adamic 2008), and Finland (Kojola et al. 2003; Kojola and Heikkinen 2006). Several studies have suggested that the dispersal and various demographic and ecological parameters of spatially expanding large carnivore populations may differ from those of stable or declining populations (Swenson et al. 1998; Bales et al. 2005). Frequent long-distance dispersal events in recovering populations likely support the establishment of metapopulations (Swenson et al. 1998) and the preservation of genetic diversity (Berthouly-Salazar et al. 2013). Information on the long-distance dispersal of bears in Greece is important, because it allows to evaluate the potential of the species to form metapopulations (Lidicker and Koenig 1996) and ultimately, to survive in the fragmented habitat of the country.

We did not detect significant differences between parent–offspring and sibling dispersal distance. However, average dispersal distance always was higher among siblings in all sex combinations. For brown bears in Scandinavia, researchers hypothesized that female littermates compete for philopatry. The authors speculated that a body size-based dominance hierarchy forced the subdominant sister to disperse (Zedrosser et al. 2007). However, this hypothesis is strongly influenced by individual body size and therefore was unable to be assessed in our study.

Our analyses on spatial autocorrelation displayed low values for relatedness, indicated however that relatedness among females autocorrelated across short distances, suggesting strong philopatry for this sex (Schregel et al. 2017). In contrast, no
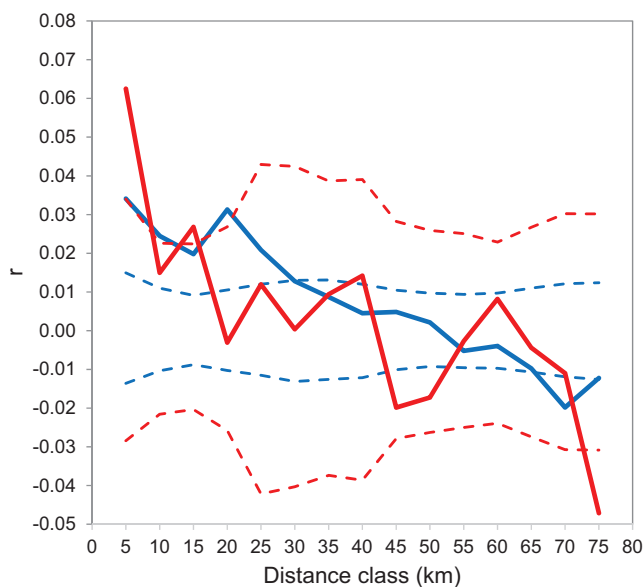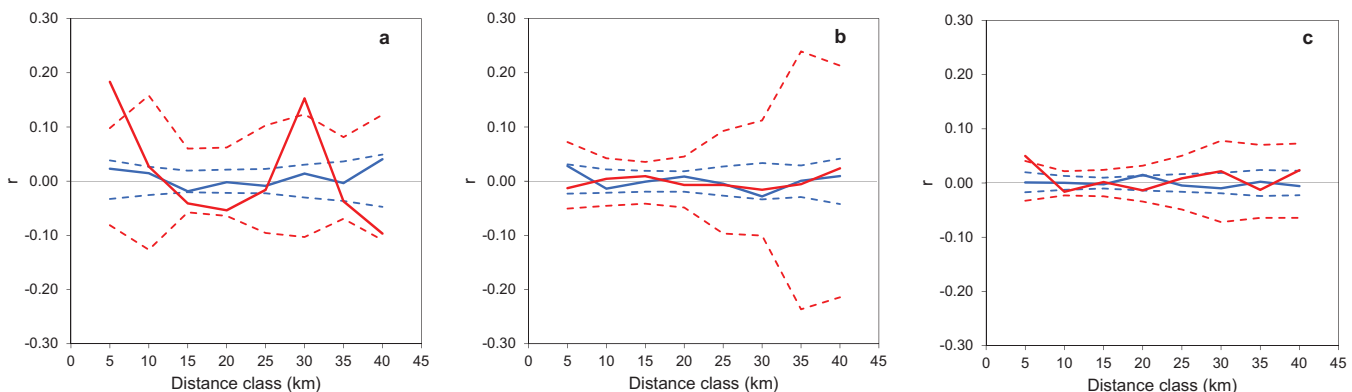

Fig. 4.—Spatial autocorrelation of female (red) and male (blue) brown bears of the three subpopulations in Greece (2003–2010) (Karamanlidis et al. 2018) based on 15 microsatellite markers, in (a) Vitsi-Varnoundas, (b) North Pindos, and (c) Central/South Pindos. The dotted line shows the 95% confidence interval for the null hypothesis of random distribution of genotypes.

relationship of kinship and geographical distance among pairs of males was found beyond a distance of 30 km. Despite the low relatedness values, this result suggests that males are the primary dispersing sex in the region. Up to a geographical distance of 30 km, males showed a spatial autocorrelation pattern that was similar to that of females in our study area, suggesting potential limitations to long-distance dispersal or also, albeit to a slighter degree than in females, male philopatry. On a more local scale, within the documented subpopulations (Karamanlidis et al. 2018), patterns of spatial autocorrelation seemed to vary, with a relationship of kinship and spatial distance at short distances indicated only for females in the subpopulations in Vitsi-Varnoundas and Central/South Pindos. We speculate that this relationship might be due to the lower sample size of females compared to males, which resulted in a lower number of pairwise comparisons and may have resulted in an underestimation of the effect of spatial autocorrelation, otherwise displayed in our analyses including kinship and distances (Banks and Peakall 2012; Schregel et al. 2017).

The situation observed in western Greece resembles the situation observed in northern Sweden, where males and females also showed spatial autocorrelation over short distances (Schregel et al. 2017). It has been suggested that in northern Sweden, mechanisms such as kin-recognition supporting the formation of family clusters might be at play that further increase territorial behavior and constitute a considerable challenge for new males entering the area to reproduce (Schregel et al. 2017). Such an effect may be influenced and/or increased by higher density of humans and levels of human activity, as is the case for Greece. Nonetheless, the observed pattern of male philopatry over short distances in Greece might be indicative of potential challenges and limitations to longer dispersal of males in the region, such as human impact by, e.g., the development of transportation infrastructure and potentially poaching. Indeed, these factors have been a cause of conservation concern for bears in Greece lately (Karamanlidis et al. 2012). Further research is required to substantiate the effects of anthropogenic barriers and human-induced mortality (e.g., illegal hunting, poisoning—Ntemiri et al. 2018) on male and female brown bear dispersal in Greece.

The dispersal patterns of bears in Greece in general and on a large scale were in accordance with the theoretical assumptions regarding dispersal, where in polygamous species, philopatry should favor the limiting sex and dispersal the other (Greenwood 1980). As in most mammals, female bears are the limiting sex and likely to gain more than males from being philopatric and familiar with the local environment. Males in contrast should benefit more than females by moving outside their natal area, to find a potential mating partner (Pusey 1987). Furthermore, dispersal distances are predicted to vary depending on the main selective driver, with shorter dispersal distances being enough to avoid resource and intraspecific competition and longer dispersal distances being necessary to avoid inbreeding (Ronce et al. 2001). Although our analysis did not permit the identification of the parent or offspring role in a specific relationship, the

average dispersal distances recorded in our study were considerably larger than the home range diameter of the average female (8 km) and male (16 km) in Greece, suggesting that dispersers had moved beyond the average home range habitually recorded in the study area (De Gabriel Hernando et al. 2020). These results are indicative of a behavior to avoid resource and intraspecific competition, but also inbreeding. "Inbreeding avoidance" has been hypothesized as the primary driver for bear dispersal in Scandinavia (Zedrosser et al. 2007).

Beyond dispersal patterns, understanding the factors influencing bear dispersal in Greece would be helpful in understanding the process of recovery of the species in the country. Dispersal in human-dominated landscapes, such as that in Greece often is influenced by factors such as bear density, habitat connectivity, or landscape barriers. The source–sink model of population dynamics predicts that density drives emigration of subordinate animals to habitats offering lower competition for resources (Stoner et al. 2013); thus, it would be reasonable to expect bears in Greece to disperse from areas with high bear density to areas of low density. In dispersing females, avoidance of aggressive interactions with males (Karamanlidis et al. 2015a) could further enhance the importance of avoiding high bear density areas. Furthermore, dispersal is an inherently spatial process that can be affected by habitat conditions in sites encountered by dispersers (Graves et al. 2014), with contiguous landscapes enabling dispersal (Stoner et al. 2013). As in the case of Florida black bears (*Ursus americanus floridanus*—Dixon et al. 2007), it should be expected that increasing habitat connectivity would positively influence bear dispersal in western Greece. In addition to the negative effects of habitat fragmentation, transportation infrastructure also may negatively affect dispersal, as shown in brown bears in Canada (Proctor et al. 2002) and Romania (Fedorca et al. 2019). The extensive road network in the study area and the two highways that have been constructed recently most likely have influenced brown bear behavior in the region. This has been documented in both males and females, who avoid suitable habitat near highways in the study area (De Gabriel Hernando et al. in press). Regular monitoring of the bear population in the region therefore should be a management and conservation priority, to potentially mitigate the negative effects of transportation infrastructure.

The brown bear population of Greece represents a recovering population that went through a historical bottleneck (Karamanlidis et al. 2018), which makes it likely that a number of individuals may display higher relatedness than one would expect in a panmictic, wildlife population (Hedrick and Kalinowski 2000). The territorial behavior of male bears, as observed in other populations, also may result in a higher number of siblings in some regions (Støen et al. 2005, 2006). To investigate that phenomenon further would require specifically targeted studies at an individual level. Age data on the sampled individuals would have been helpful, but most genotypes originated from noninvasively collected samples for which an age estimation was not possible. However, a recent, comparable study applying FAMILIAS to assess first-order relationships based

on microsatellite genotypes supports that our results of parent–offspring and sibling relationships applying a cutoff value of LR ≥ 20 are accurate (Holmala et al. 2018). Our cutoff value for LR might be lower than recommended by some studies; however, our results were conclusive and a LR of 20 and above is considered as moderate support for the proposed relationship (Willis et al. 2015). While the inclusion of potentially immature brown bears may bias the results, our study nonetheless provides an overall picture on the dispersal patterns of brown bears in a human-dominated landscape.

The results of our combined approach of using kinship and a summarizing spatial autocorrelation analysis highlighted the limitations of the latter when applied to subgroups. Previous studies have shown that analyses on spatial autocorrelation of geographically restricted subpopulations may potentially underestimate the strength of the genetic–geographic distance relationship (Banks and Peakall 2012; Schregel et al. 2017). This likely is caused by the exclusion of genetically admixed individuals, which often are found between groups and regions where individuals from different subunits meet. Further, such an effect may be especially pronounced when the available data are scarce, as for bears sampled in the separate, local regions in our study, and results therefore may remain inconclusive by resulting also to low values for relatedness. Nonetheless, the effect of spatial autocorrelation among all bears in our study was a significant relationship for both sexes, which may point to challenges for bears on a more local scale. We propose further investigation of the local subpopulations of the Greek brown bear by producing genetic data of higher resolution (Norman and Spong 2015) and possibly to include data on bear movement (Støen et al. 2005, 2006; Zedrosser et al. 2007) to illuminate local relationships among brown bears.

Given the discussed limitations, our study is one of the few to assess dispersal of brown bears in a human-dominated landscape, which would not have been possible without the collection of noninvasive samples. Our study also shows that kinship analyses with prior evaluation of the genetic marker system is able to provide additional important and valuable insights. While more sampling effort and studies are necessary, we provide previously lacking information for the understanding of the dispersal behavior of brown bears in Greece. This is important not only for understanding the processes behind the successful recovery of a large carnivore in a human-dominated landscape, but also for predicting the potential of the species to deal with the effects of climate change. With the effects of climate change in Greece expected to be particularly intense (Giannakopoulos et al. 2009) and bear activity negatively affected by increasing temperatures (De Gabriel Hernando et al. 2020), it is the dispersal behavior of the species that ultimately will determine whether it will be able to disperse fast or far enough to track shifts in suitable climates and associated habitats (Schloss et al. 2012).

Acknowledgments

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data.—Supplementary data/information on the methodology used to evaluate the genetic marker system used in the study to evaluate kinship of brown bears in Albania, Greece, and Northern Macedonia.

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