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Spatio-temporal movement patterns of brown bears (*Ursus arctos*) in the Central Balkans

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Prostorno-vremenski obrasci kretanja mrkog medveda (*Ursus arctos*) na centralnom Balkanu

- doktorska disertacija -

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Spatio-temporal movement patterns of brown bears (*Ursus arctos*) in the Central Balkans

ABSTRACT

Humans are changing their environment, either directly through habitat modifications or indirectly by changing climatic conditions. These changes have made habitats less suitable for wildlife, thereby prompting many species to modify their behavior and phenology. In addition, the rapid development of the transportation network has led to a tremendous reduction in landscape connectivity, making it difficult for many species, especially those with large spatial requirements, to satisfy their needs. Brown bears are the most widespread of all bear species and their populations are slowly recovering and expanding into human-modified landscapes. As apex predators with home ranges up to several thousand square kilometers, brown bears represent a particularly interesting model species to study the effects of humans and their activities on wildlife behavior. The main focus of this doctoral dissertation was to analyze whether and to what extent brown bears change their movement ecology (i.e. seasonal and diel movement patterns), hibernation behavior and habitat preference in response to human-induced disturbance, habitat modifications, but also climate change.

The results revealed that bears exhibit a bimodal activity pattern with the highest movement rates during crepuscular and night hours, although significant variation was observed within the population and throughout the year (i.e. between seasons). In general, females with dependent offspring and subadult males altered their movements (i.e. became more diurnal or dispersed) in response to male conspecifics, confirming a significant influence of intraspecific social dynamics (avoidance of infanticide and inbreeding) on the brown bear movement ecology. All bear classes except females accompanied by offspring decreased their movement rates towards the hyperphagia season, implying the possible influence of feeding stations on bear behavior. Furthermore, significant variability in winter behavior was observed across 31 analyzed winter events. The results showed that the abundant human-provided food resources in the study area during winter favored the coexistence of four different wintering strategies: obligate hibernation with individuals hibernating for the entire winter for females with offspring of all ages; facultative hibernation in which non-reproductive individuals hibernate throughout the winter; facultative intermittent hibernation with short periods of activity; and complete activity. In addition, winter active bears significantly reduced their movement as snow depth increased and showed higher fidelity to supplementary feeding sites, especially during the winter months. Therefore, the observed results in combination with global warming suggest that the use of hibernation as a strategy to overcome food shortages during winter might decrease in the future. Finally, the species' distribution modeling highlighted that more than 60% of the identified suitable areas are still available for brown bear populations to increase in size and range, with higher elevation areas and dense forest cover being the most important factors in habitat selection for bears. In addition, more than half of the bear occurrences were located inside the protected areas, indicating their important role in brown bear conservation. The „Radan Mountain" Nature Park is highlighted as a particularly important connectivity area, as it can promote movement of bears from the Dinaric-Pindos population to the Eastern Balkan and Carpathian populations, and vice versa. However, it is necessary to implement adequate mitigation measures to increase the

habitat permeability. Considering that human influence on nature is expected to grow in coming years, the results of this doctoral dissertation will be a keystone on which future national conservation and management strategies should be built.

Key words: Brown bear, movement patterns, hibernation, supplementary feeding, climate change, winter activity, habitat preference, population connectivity

Scientific field: Ecology
Scientific subfield: Ecology, biogeography and nature conservation

Prostorno-vremenski obrasci kretanja mrkog medveda (*Ursus arctos*) na centralnom Balkanu

SAŽETAK

Ljudi su oduvek imali tendenciju da sebi prilagođavaju neposredno okruženje. Ipak, u poslednjih par decenija, svedoci smo da je priroda planete Zemlje pretrpela drastične izmene, ali i da će potrebe sve veće ljudske populacije nastaviti da oblikuju izgled naše planete u budućnosti. Ljudi su kako direktnim (modifikacija staništa) tako i indirektnim (klimatske promene) promenama doveli do toga da mnoga staništa postanu manje povoljna za divlje životinje, što za posledicu ima značajne izmene u njihovom ponašanju. Osim toga, intenzivan razvoj infrastrukturne mreže doveo je do drastične fragmentacije staništa, što je mnogim vrstama, a naročito onim sa velikim prostornim zahtevima, u velikoj meri otežalo zadovoljavanje osnovnih životnih potreba.

Mrki medvedi su na globalnom nivou najšire rasprostranjena vrsta medveda, čije se populacije polako oporavljaju i sve više zalaze u ljudski-modifikovana staništa. Kao vršni predatori, mrki medvedi mogu imati teritorije i po nekoliko hiljada kvadratnih kilometara, što ih čini naročito pogodnom model vrstom za ispitivanje uticaja čoveka i njegovih aktivnosti na ponašanje, aktivnost i kretanje divljih životinja. Ovakva saznanja su od izuzetnog značaja za omogućavanje koegzistencije ljudi i divljih životinja. Stoga, fokus ove doktorske disertacije je kako mrki medvedi reaguju na antropogene promene u staništima koja naseljavaju na prostoru centralnog Balkana. Pre svega, cilj je bio da se utvrdi efekat antropogenog uznemiravanja, uništavanja staništa, ali i klimatskih promena na obrasce kretanja i aktivnosti medveda (na dnevnom i sezonskom nivou), kao i na hibernacijsko ponašanje i preferenciju staništa.

Prva studija je pokazala da medvedi imaju bimodalni obrazac kretanja sa najvećim stopama kretanja tokom noći i sumraka, pri čemu su zabeležene značajne unutarpopulacione i sezonske razlike. Generalno, kod ženki sa potomstvom i subadultnih mužjaka zabeležene su značajne razlike u obrascima kretanja (postali su više dnevno aktivni ili su dispergovali) kao odgovor na agresivne mužjake, što potvrđuje značajan uticaj unutarpopulacione socijalne dinamike (izbegavanje infanticida ili inbridinga) na obrasce kretanja medveda. Osim toga, sve klase (adultni mužjaci, subadultni mužjaci i solitarne ženke) medveda izuzev ženki sa potomstvom (verovatno kao posledica veće mobilnosti i nutritivnih potreba mečića) su značajno smanjile stopu kretanja tokom sezone hiperfagije, ukazujući na potencijalni efekat koji hranilišta mogu imati na ponašanje medveda. U okviru druge studije, analize zimskog ponašanja medveda ukazale su na značajne razlike u ispoljavanju hibernacije između medveda različitog starosnog i reproduktivnog statusa. Od 31 analiziranog zimskog perioda, 25 je identifikovano kao hibernacija, i to kao jedinstvena (6 slučajeva) ili isprekidana (do pet perioda mirovanja) hibernacija (19 slučajeva). Generalno, mužjaci su provodili značajno manje vremena (~80 dana) u brlogu u odnosu na ženke (~128 dana), dok su među ženkama različitog reproduktivnog statusa, ženke sa tek okoćenim mečićima hibernirale najduže (~155 dana). Pored toga, dobijeni rezultati su pokazali da u toku 6 zimskih perioda, medvedi (sve mužjaci) nisu pokazali ponašanje koje odgovara hibernaciji. U tri slučaja, medvedi su pokazali semi-aktivno ponašanje (sa 30 ili manje dana mirovanja), dok su u druga tri slučaja, medvedi bili konstantno aktivni tokom cele zime. I pored toga, svi medvedi koji su pokazali aktivnost preko zime su značajno

smanjili kretanje sa porastom dubine snega (sa 2,5 km/dan kada nije bilo snega, na 1,1 km/dan pri 50 cm dubokom snegu). Osim toga, dobijeni rezultati su ukazali na to da praksa dodatnog prihranjivanja medveda dovodi do većeg privikavanja medveda takvim mestima, naročito tokom zimskih meseci. Shodno tome, rezultati su pokazali da su u januaru aktivni medvedi provodili ~50% svog vremena u blizini hranilišta, u poređenju sa svega 10% u junu i julu. Prema tome, velika količina hrane koju obezbeđuje čovek u našem području tokom zime se može smatrati glavnim razlogom za pojavu različitih strategija prezimljavanja kod medveda, što u kombinaciji sa klimatskim promenama i rastom prosečnih mesečnih temperatura može smanjiti učestalost hibernacije u budućnosti. U trećoj studiji, modelovana je distribucije vrste na dve prostorne skale (5 i 1 km²) kako bi se identifikovala povoljna staništa gde bi medvedi potencijalno mogli da šire svoj areal na teritoriji Srbije. Dobijeni rezultati pokazali su da veće nadmorske visine i gusto obrasla šumska staništa predstavljaju najbitnije faktore u izboru staništa medveda, pri čemu su zabeležene izvesne razlike između različitih populacija medveda prisutnih na prostoru Srbije. Za razliku od dinarsko-pindske populacije medveda kod kojih je nadmorska visina najbitnija sredinska varijabla, karpatska populacija medveda mnogo više zavisi od prisustva šumskih staništa (što se može tumačiti manjim nadmorskim visinama u istočnoj Srbiji). Osim toga, dobijeni rezultati su potvrdili da medvedi trenutno zauzimaju samo mali deo identifikovanih povoljnih staništa (35,4 i 24,4% na gruboj, odnosno finoj skali), ostavljajući više od 60% povoljnih staništa gde populacije medveda mogu širiti areal i povećavati svoju brojnost. Takođe, više od polovine podataka o prisustvu medveda nalazi se unutar zaštićenih područja, što ukazuje na njihov veliki značaj za zaštitu i očuvanje medveda. Iako povezanost i protok gena između tri prisutne populacije medveda nije registrovana do sada, rezultati su pokazale da postoji nekoliko područja, pre svega u južnom i jugoistočnom delu zemlje, gde može doći do uspostavljanja funkcionalne povezanosti sve tri populacije u budućnosti. Park prirode "Radan" je označen kao naročito važno područje, gde se može očekivati kretanje jedinki iz dinarsko-pindske populacije medveda prema istočno balkanskoj i karpatskoj populaciji, i obrnuto. Međutim, ovo područje je ispresecano sa nekoliko barijera (autoput, železnica, dolina Morave) koje značajno ometaju kretanje medveda, ali i drugih životinja. Stoga, ovi rezultati mogu poslužiti kao vodič za identifikovanje lokacija na kojima bi uspostavljanje mitigacionih mera bilo najefektivnije za unapređenje prohodnosti staništa.

Ova doktorska disertacija predstavlja prvu sveobuhvatnu analizu obrazaca kretanja medveda u Srbiji. Prezentovani rezultati potvrdili su da su antropogene promene životne sredine uzrokovale značajne prostorno-vremenske izmene u obrascima kretanja i ponašanju medveda. Kako se očekuje da će uticaj ljudi na prirodu da raste u budućnosti, rezultati ove disertacije predstavljaju osnovu na kojoj se mogu bazirati buduće nacionalne konzervacione i upravljačke strategije.

Ključne reči: mrki medved, obrasci kretanja, hibernacija, dodatno prihranjivanje, klimatske promene, zimska aktivnost, preferencija staništa, populaciona povezanost

Naučna oblast: ekologija
Uža naučna oblast: ekologija, biogeografija i zaštita životne sredine

CONTENT

I INTRODUCTION

1. Living in a changing world – effects of human disturbance and climate change on wildlife behavior

The world has begun to change rapidly in recent decades. A significant increase in human population together with intense urbanization and climate change have led to immense alterations in the Earth's environment. The vast majority of once natural ecosystems have now been transformed into a network of areas intended to meet the needs of a growing humanity (often referred to as the Anthropocene) (Waters *et al.*, 2016). As a result of human encroachment, there are few ecosystems left that have not been modified, exploited, fragmented or polluted (Walther *et al.*, 2002; Isaac, 2009). According to the World Database on Protected Areas, only ~24% of the world's surface is under some form of protection, of which 16% occur within terrestrial areas and inland waters (UNEP-WCMC, 2024). However, most of these protected areas are not very large and are scattered within highly modified anthropogenic environments, indicating that the implementation of protective measures outside of these areas will also become crucial for long-term sustainable conservation. Furthermore, global warming is already affecting life on Earth, and these changes are expected to become even more pronounced in the future. According to the latest estimate by the Intergovernmental Panel on Climate Change (IPCC, 2023), global temperatures are expected to further increase during the 21st century, with extreme events such as wildfires, floods and hurricanes becoming more frequent. The gradual increase in global temperatures combined with changes in other aspects of climate, such as rain and snow, is expected to alter plant phenology, which in turn will challenge animal species to satisfy their food requirements, leading to a mismatch between plant and animal phenology (Walther *et al.*, 2002; Visser & Both, 2005). With the increase in average temperatures (IPCC, 2023), many species that live in temperate environments are expected to expand their distributions towards the poles or to higher altitudes (Hickling *et al.*, 2006), while species that are not as adaptable will experience range loss (Thomas, Franco & Hill, 2006). It is difficult to predict how these global changes will manifest on a smaller scale and how wildlife will respond to these spatially heterogeneous changes (Walther *et al.*, 2002; Thomas *et al.*, 2004). Ultimately, species could become extinct if they cannot adapt to the new environmental conditions or disperse into habitats with suitable conditions in which they can survive.

1.1. Challenges for large mammals in a changing world

Mammals are severely threatened by human-induced changes to the Earth's climate and ecosystems, although the threat levels vary between mammal groups. In general, larger mammals face greater risk because they often exist in lower population densities and require larger areas to fulfill their life cycle (Schipper *et al.*, 2008). Under conditions where climate change is occurring too fast and human-caused habitat modification is too widespread, species have three options: a) to shift their distribution to more favorable areas, b) remain in the same area and adapt to the newly created environmental conditions, or c) become extinct (Hetem *et al.*, 2014). Given that the potential for range shifts within human-modified landscapes is limited for large mammals, a species' ability to adapt to the changing

environment will be crucial to determine its fate in the future. Large carnivores such as bears, wolves and lynx attract considerable attention in relation to human-caused environmental changes, as they are often considered umbrella or keystone species (del Rio *et al.*, 2001; Treves & Karanth, 2003; Kittle *et al.*, 2018; Helman, Zarzo Arias & Penteriani, 2022). Due to centuries of persecution by humans and immense changes to their habitats and prey abundance, many large carnivore populations worldwide have been driven to the brink of extinction (Breitenmoser, 1998; Woodroffe, 2000; Linnell, Swenson & Andersen, 2001). However, thanks to advances in conservation, we are currently witnessing the recovery of some large carnivore populations and the recolonization of some parts of their former ranges in Europe (Chapron *et al.*, 2014). Nevertheless, large areas that used to be their natural habitats have been transformed into human-modified landscapes (Vitousek *et al.*, 1997), suggesting that humans and large carnivores are in recurrent competition for resources within a shared space (Treves & Karanth, 2003). Therefore, establishing coexistence between humans and wildlife while minimizing the negative impacts they have on each other is a major issue and priority for biodiversity conservation in the Anthropocene.

1.1.1. Humans as a cause of changes in mammals

Many ecosystems are affected by humans and their activities, which threaten the survival of many species worldwide. According to Ceballos *et al.* (2015), human-related activities have caused many mammal species to halve their distributional ranges worldwide. Tucker *et al.* (2018) have shown that the movement of more than 50 mammal species is significantly reduced in areas with a high human footprint. In addition, large-bodied mammals with long lifespans are often more affected by human-caused landscape alterations compared to smaller species (Hill *et al.*, 2020). Large carnivores often occupy the top position of food chains in many ecosystems. Through predator-prey interactions, they play a key ecological role in controlling both the numbers and behavioral responses of species at lower trophic levels (Laundré, Hernández & Ripple, 2010; Ordiz *et al.*, 2021). As apex predators, they have no natural enemies, which means that their abundance is controlled either by prey availability and habitat suitability or by humans, who act as "super-predators" in many ecosystems (Dorimont *et al.*, 2015). Thus, a decline in large carnivore populations due to anthropogenic threats can lead to a release of prey species with far-reaching consequences for the entire ecosystem (Ordiz *et al.*, 2021). However, despite immense human-caused habitat modification, particularly in Europe, most large carnivore species succeeded to reclaim large part of their former distribution (Chapron *et al.*, 2014). Such remarkable success emphasizes the huge efforts that have been invested in the conservation of both large carnivores and their habitats in recent years, but also shows that large carnivores have made significant behavioral adaptations which enable them to successfully coexist with humans (Ordiz *et al.*, 2021).

1.1.1.1. Human disturbances

Coping with increased levels of human disturbances represents one of the greatest challenges for large carnivores in human-modified landscapes (Ripple *et al.*, 2014; Ordiz *et al.*, 2021). As a response to anthropogenic disturbance, it has been suggested that large carnivores have undergone significant behavioral changes that enable them to avoid humans both spatially and temporally (Martin *et al.*, 2010; Ordiz *et al.*, 2011, 2021; White *et*

al., 2015). These responses developed as a trade-off between fulfilling nutritional requirements while reducing direct contact with humans, mostly by adjusting space-use patterns (May *et al.*, 2006; Martin *et al.*, 2010; Lesmerises, Dussault & St-Laurent, 2012; Ordiz *et al.*, 2017; Gaynor *et al.*, 2018; Mancinelli, Boitani & Ciucci, 2018; Milleret *et al.*, 2018). Many studies have shown that carnivores' habitat selection is primarily determined by spatial avoidance of human encounters, which results in choosing densely forested or steeper terrain away from humans (Martin *et al.*, 2010; White *et al.*, 2015; Milleret *et al.*, 2018; De Angelis *et al.*, 2021). Furthermore, nocturnality in many carnivore species emerged as a fear response to human disturbance (Gaynor *et al.*, 2018). In fact, in environments dominated by mostly diurnal humans, being nocturnal enhances the chances for survival but also favors the human-carnivore coexistence.

1.1.1.2. Habitat fragmentation and degradation

Changes in human land use (e.g. forestry, agriculture, urbanization) have permeated into the even most remote ecosystems, and in the last six decades alone, approximately 30% of the worlds land surface has experienced a change in land use (Winkler *et al.*, 2021). An additional consequence of land use change is habitat fragmentation, i.e. transformation of large, continuous natural habitats into a series of smaller patches isolated from each other by a mostly unsuitable habitat matrix (Fahrig, 2003), ultimately leading to a significant reduction in landscape connectivity (Haddad *et al.*, 2015; Wilson *et al.*, 2016). The loss of functional connectivity across the landscape represents one of the biggest threats to biodiversity today, especially for mammals with huge spatial requirements, such as large carnivores (Dixon *et al.*, 2007; Cushman *et al.*, 2013; Mateo-Sánchez, Cushman & Saura, 2014; Crooks *et al.*, 2017; Thatte *et al.*, 2020). Due to long-term human-caused habitat degradation, many large carnivore species have experienced severe range constrictions or population declines and often persist only in metapopulations (i.e. isolated populations scattered across the fragmented landscape) (Ordiz, Bischof & Swenson, 2013a; Ripple *et al.*, 2014; Wolf & Ripple, 2017; Penteriani *et al.*, 2018). Under such circumstances, the lack of connectivity between metapopulations restricts gene flow and thus reduces genetic diversity within populations. Such reduced genetic diversity can make small isolated populations more susceptible to stochastic events and extinction (Dixon *et al.*, 2007; Mateo-Sánchez *et al.*, 2014; Crooks *et al.*, 2017; Thatte *et al.*, 2020). This can be further reinforced by highly developed road infrastructure, which fragments habitat and causes animals to change their movements. Under such conditions, the probability of finding mates, shelter and food resources decreases significantly, with devastating consequences for the entire populations (Trombulak & Frissell, 2000; Proctor *et al.*, 2012; Bischof, Steyaert & Kindberg, 2017; Skuban *et al.*, 2017; Penteriani *et al.*, 2018).

1.1.1.3. Management practices

Large carnivores are at the top of the food chain in all terrestrial ecosystems and exert a profound influence on their biological communities through predation and interspecific competition (Berger *et al.*, 2001; Treves & Karanth, 2003). However, their ecological role in the ecosystem has changed dramatically due to centuries of persecution by humans and global decline in both abundance and distribution of large carnivores (Ordiz *et al.*, 2013a; Ray *et al.*, 2013; Terborgh & Estes, 2013). Although their conservation importance as flagship and umbrella species (Sergio *et al.*, 2008) emphasizes the urgent need for well-planned wildlife management policies, the large carnivores conservation has always been

controversial. In general, the conservation of these species is often closely related to socio-economic conflicts with humans, mostly arising from the loss of livestock and game species, damage to property, but also due to occasional attacks on people (Stahl *et al.*, 2001; Packer *et al.*, 2005; Sergio *et al.*, 2008; Ordiz *et al.*, 2013a; Penteriani *et al.*, 2016). Therefore, different countries have adopted different population management systems to deal with such conflicts while ensuring the long-term conservation of large carnivores (Bautista *et al.*, 2019). Hunting is commonly used as a conflict-reducing management tool, although its indirect consequences can jeopardize carnivore populations if harvest is too high, e.g., by reducing genetic diversity or disrupting of social organization (Creel *et al.*, 2015; Bischof *et al.*, 2018; Penteriani *et al.*, 2018; Van De Walle *et al.*, 2018; Ordiz *et al.*, 2021). Another ubiquitous management practice is the intentional provision of food to wildlife (i.e. supplementary or diversionary feeding). Supplementary feeding is used for various purposes, such as population recovery, hunting, ecotourism, research and human-carnivore conflict mitigation (Selva, Berezowska-Cnota & Elguero-Claramunt, 2014; Selva *et al.*, 2017). However, by increasing the availability and predictability of food subsidies, humans have triggered many undesirable effects on both wildlife and ecosystems, such as changes in trophic cascades, movement and activity patterns, social interactions, reproductive behavior, hibernation phenology, as well as disease transmission (Selva *et al.*, 2014, 2017; Sorensen, van Beest & Brook, 2014; Newsome *et al.*, 2015; Bojarska *et al.*, 2019). Today, due to the development and implementation of conservation-oriented management policies, many large carnivores are recovering and expanding into heavily modified habitats. This suggests that future conservation efforts must take place in human-dominated landscapes to ensure the long-term carnivore persistence while permitting sustainable socio-economic development for humanity (Boitani, 2000; Linnell *et al.*, 2001; Treves & Karanth, 2003; Zedrosser *et al.*, 2011; Chapron *et al.*, 2014).

1.1.2. Effects of global warming on mammals

Human-induced climate change is one of the greatest threats to biodiversity. As a result of pronounced warming, the distribution of vegetation is shifting to higher altitudes (Walther *et al.*, 2002), leading to changes in the geographical and altitudinal distribution of many mammals (Isaac, 2009). This can be particularly detrimental to species with specific habitat requirements, as limiting these species to less suitable habitats can lead to fragmentation of population, which in turn makes them highly sensitive to stochastic events (Isaac, 2009). According to Thomas *et al.* (2004), 15 to 37% of species, including mammals, will be lost by 2050. Previous studies have shown that global climate change climate affects mammals by causing significant alterations in their abundance, distribution, phenology, but also in their behavior (Boutin & Lane, 2014; Hetem *et al.*, 2014; Beever *et al.*, 2017). In general, even subtle changes in a species' abiotic environment, such as changes in temperature, precipitation and the occurrence of extreme events (i.e. floods, droughts, hurricanes, etc.), are expected to directly affect the species' reproduction and survival rates (Humphries, Umbanhowar & McCann, 2004). Beever *et al.* (2017) found that most of the analyzed taxa, including mammals, commonly responded to a warming climate with changes in reproductive behavior (i.e. advancing birth dates; Boutin & Lane, 2014) and movement (i.e. dispersal and migration). However, as the ability of species to disperse or migrate depends on its movement capacity, some mammals will not be able to keep pace with rapid climate change. According to Schloss *et al.* (2014) almost 10% of mammals in the western hemisphere will

be unable to shift their range to more favorable habitats. In such a scenario, the survival of species will depend on their ability to adapt genetically to environmental changes. However, as evolutionary change is too slow compared to the rate of climate change, it is expected that some mammals, especially those with long gestation and generation times such as large mammals, will not be able to respond genetically fast enough (Boutin & Lane, 2014). Furthermore, climate-induced changes in the abundance and distribution of resources can have extremely negative consequences for large mammals. In particular, milder winters with shorter period under snow, can lead to an earlier vegetation green up in the following spring, especially in temperate and polar regions (Post *et al.*, 2001). This can be particularly detrimental to hibernating species, as it can lead to a mismatch between hibernators and their important food resources both prior and upon emergence from hibernation (Inouye *et al.*, 2000; Durant *et al.*, 2005; Penteriani *et al.*, 2019), and ultimately affect a species' reproductive success.

2. Brown bear as model species for assessing anthropogenic pressure on the large carnivore behavior

Due to their secretive lifestyle and charismatic nature, bears have been the subject of intensive research for decades (Swenson *et al.*, 2000; Steyaert *et al.*, 2012; Penteriani *et al.*, 2018; González-Bernardo *et al.*, 2020). Bears are large terrestrial omnivores, which makes them particularly important for maintaining the stability of the entire ecosystem, through complex trophic cascade processes (Sergio *et al.*, 2008; Ordiz *et al.*, 2021). Compared to other bear species, brown bears (*Ursus arctos*) have the widest geographic distribution, spanning the entire northern hemisphere across Europe, Asia and North America, and are often highlighted as umbrella and flagship species within their ecosystems (Sergio *et al.*, 2008). However, as human encroachment into brown bear habitats increases, so does the impact of human activities and infrastructure on bear populations worldwide (Nellemann *et al.*, 2007; Ordiz *et al.*, 2011, 2021; Støen *et al.*, 2015; Penteriani *et al.*, 2018; Morales-González *et al.*, 2020). Although bears require large areas to fulfill their needs and are extremely timid when disturbed by humans (Ordiz *et al.*, 2011), they can survive and even increase in numbers in coexistence with humans in Europe (Chapron *et al.*, 2014; Elfström *et al.*, 2014; Zarzo-Arias *et al.*, 2019). However, considering that bears have to compete with humans for the same space and resources in human-modified landscapes, understanding how bears will adjust their behavior in relation to humans, but also the attitude of humans towards sharing their habitats with large animals such as bears, is attracting much attention in the scientific community.

2.1. Brown bear morphology

The brown bear is a terrestrial omnivore belonging to the order Carnivora. It is a large-bodied animal with a massive head, relatively small, rounded ears and a short, unnoticeable tail (Figure 1) (Heptner *et al.*, 1967). The body is covered with a thick, coarse fur, whose color can vary from light brown to almost black. Both the hind and forefeet are characterized by long, slightly curved claws intended mainly for defense, but also for killing prey. There are substanial differences between the sexes when it comes to body size (i.e. sexual dimorphism), with males being 1.2 - 2.2 times larger compared to females of the same age (Heptner *et al.*, 1967; Swenson *et al.*, 2007). Brown bear mass fluctuates throughout the course of the year due to the species' phenology (see section 2.4) as well as with latitudinal cline (i.e. geographicaly) (Meiri, Yom-Tov & Geffen, 2007; Garshelis, 2009). In general, the body mass of adult brown bears can vary from 80 kg to more than 600 kg and it is largely associated with food availability and composition (Hilderbrand *et al.*, 1999; Swenson *et al.*, 2000). Brown bears are known as facultative hibernators, with all age and sex classes hibernating for at least part of the winter, with northern populations spending significantly more time in dens compared to their southern counterparts (González-Bernardo *et al.*, 2020).

Figure 1. GPS-collared male brown bear from Zlatibor Mountain, Serbia
(author: Bogdanović, N.)

2.2. Brown bear distribution

The brown bear is the most widespread of all eight bear species and has a Holarctic distribution (Figure 2) (Swenson *et al.*, 2000; McLellan *et al.*, 2017). Although its former distribution included the entire Europe, Asia, a large part of North America, Mexico and even North Africa (Atlas Mountains), brown bears have disappeared in many countries due to high persecution pressure and habitat destruction. Today, brown bears are found in the northwestern part of North America, parts of Europe and Russia, while some small and isolated subpopulations still remain in several Asian countries (Zedrosser *et al.*, 2011; McLellan *et al.*, 2017) (Figure 2). Brown bears occupy the widest range of habitats within the Ursidae family, from dry Asian steppes, deserts (Gobi Desert, Mongolia) and temperate forest regions up to cold Arctic shrublands (McLellan *et al.*, 2017). However, in many areas within their distributional range, bears are forced to coexist with humans in heavily modified landscapes. In Europe, the distribution of brown bears is highly fragmented, resulting in 10 isolated populations within 22 countries: the Scandinavian, Karelian, Baltic, Carpathian, Dinaric-Pindos, Eastern Balkan, Alpine, Central Apennine, Cantabrian, and Pyrenean populations (Kaczensky *et al.*, 2012; Chapron *et al.*, 2014) (Figure 2). Moreover, in Central and Southern Europe, bear presence is limited to mountain ranges such as the Alps, the Apennines, the Dinaric Mountains, the Pindus and the Carpathians, as their reduced accessibility ensures low disturbance by humans. Although their former distribution

indicates the species' high adaptability (Figure 2), today, brown bears in Europe predominantly occupy forested and mountainous areas that provide enough food resources, shelters and dens and are characterized by low human activity (Swenson *et al.*, 2000). According to the International Union for Conservation of Nature (IUCN, 2012), brown bears are considered a Least Concern species at the global level (McLellan *et al.*, 2017), although the species' conservation status may vary at the country level across its distribution range, particularly in Europe (Kaczensky *et al.*, 2012).
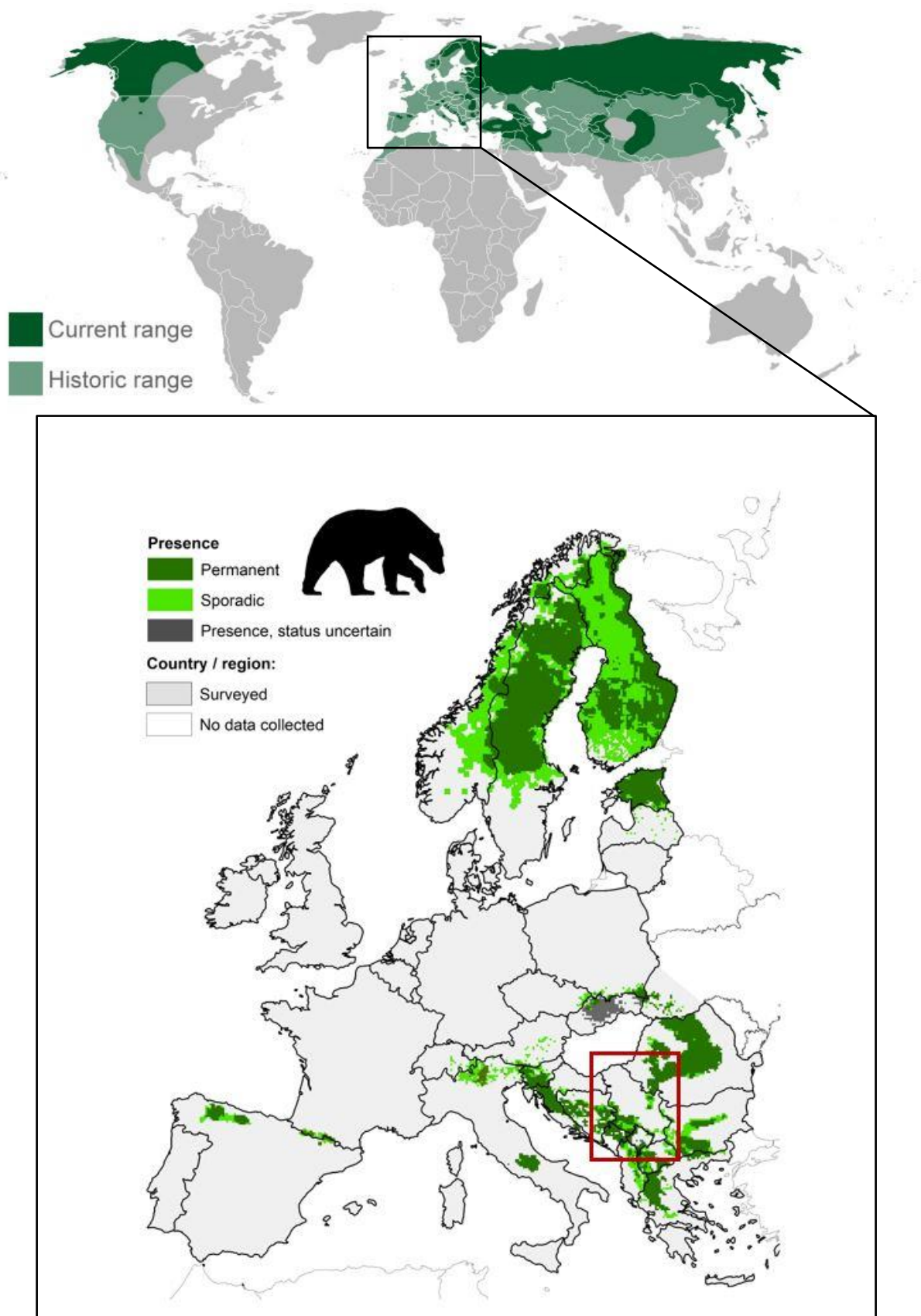
Figure 2. Distribution of the brown bear in the world, showing its historical and current range (upper map; www.ecoclimaxs.com) and its European distribution, showing the permanent and sporadic presence of the brown bear in 10 different populations (lower map; Kaczensky *et al.*, 2021). The red rectangle indicates the broader study area.

2.2.1. Brown bears in Serbia – at the crossroads of three subpopulations

Serbia is the only European country whose territory is inhabited by three different European brown bear populations (Figure 3). The Dinaric-Pindos population is located in the western and southwestern part of the country and is the most numerous of all three with ~100 individuals (Ćirović & Paunović, 2018). Individuals from the other two subpopulations are found in eastern Serbia. Approximately 6 to 10 individuals belonging to the Carpathian subpopulation inhabit the eastern part of the country, while the Eastern Balkan subpopulation, which is the smallest (estimated to be only a few (3-6) individuals), is registered in the southeast (Kaczensky *et al.*, 2012; Ćirović & Paunović, 2018). Currently, these three populations are isolated, but Serbia represents a crucial area for potential future connectivity and the establishment of gene flow between the Dinaric-Pindos, Carpathian and Eastern Balkan populations. Bears in Serbia inhabit mainly forested and mountainous areas with low human densities. Such areas are often located within protected regions, which are characterized by high-quality habitats that provide sufficient food and shelters. Until the last decade of the 20th century, the brown bear was hunted in Serbia, but in 1992 it was permanently protected by a hunting ban. Given the slow population recovery, the species' status was changed in 2010 and bears were declared a strictly protected species under Serbian national legislation (Official Gazette RS, 47/2011). Since then, considerable efforts have been made to protect brown bears and the latest population estimate indicated that all three populations are showing increasing trends, with individuals slowly spreading towards central Serbia (Ćirović & Paunović, 2018). Currently, it is estimated that the number of bears in Serbia has doubled compared to two decades ago.
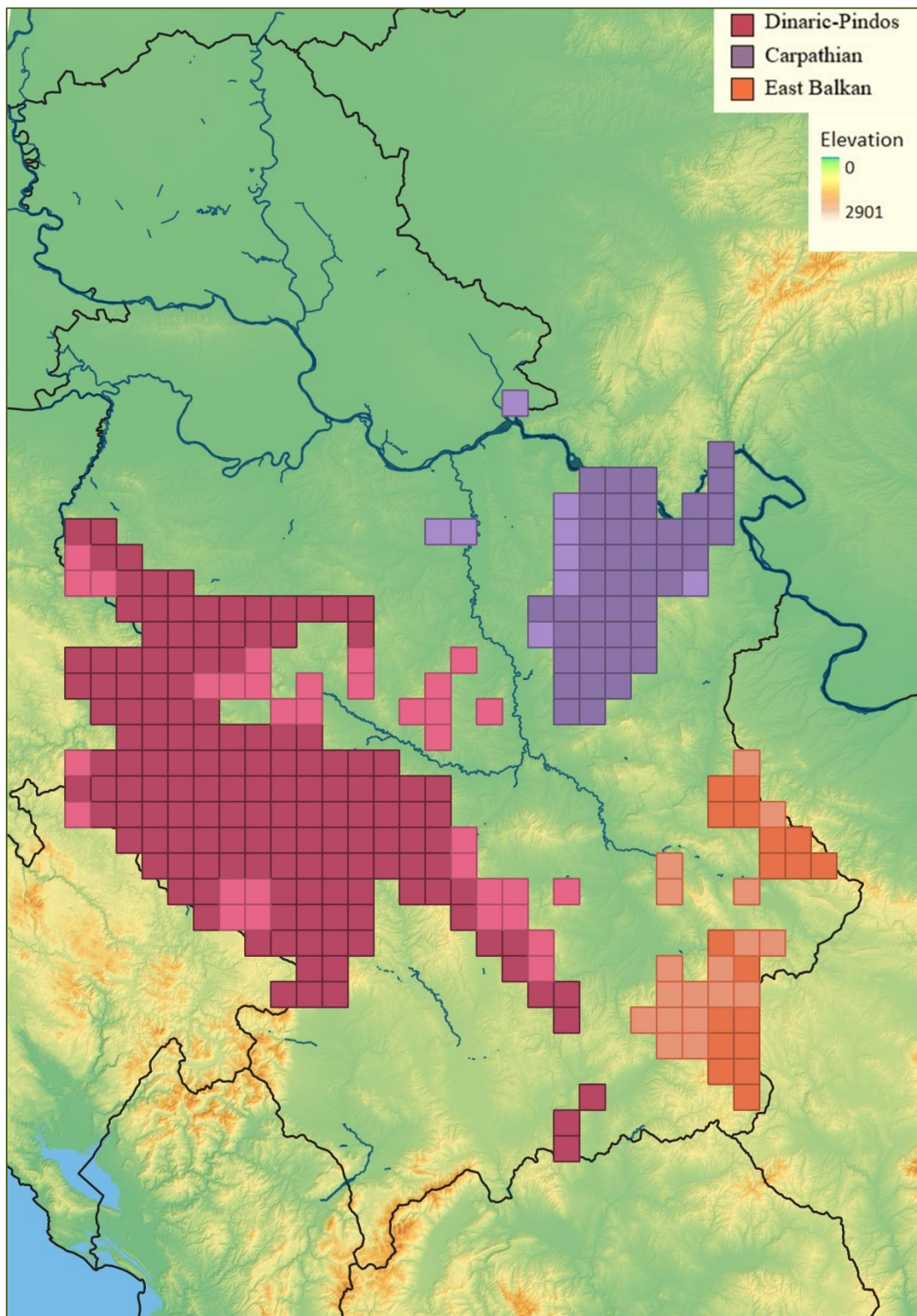
Figure 3. Distribution of three brown bear populations (green - Dinaric-Pindos, red - Carpathian and brown – Eastern Balkan) in Serbia with confirmed (darker colors) and potential (lighter colors) bear presence

2.3. Brown bear life history

2.3.1. Brown bear reproduction

Brown bears are characterized by a polygynous mating system and mating takes place from mid-May to early July (Steyaert *et al.*, 2012). Sexual maturity occurs in the third year at the earliest, both in males and females (Frković, Huber & Kusak, 2001; Zedrosser, Rauer & Kruckenhauser, 2004), with older males being more reproductively successful than younger individuals due to their dominance and experience (Zedrosser *et al.*, 2007a). Both sexes can mate with more than one partner during the mating season, which is why multiple paternity is often observed in brown bears (Bellemain, Swenson & Taberlet, 2006). Considering their higher investment in gametes and rearing offspring, female mate choice affects male reproductive success and is therefore governed by male qualities (i.e. age, size, dominance, fighting ability, etc.) (Steyaert *et al.*, 2012). Implantation in brown bears is delayed, i.e. the fertilized egg remains dormant in the uterus for about five months after fertilization (usually until November-December). After this period, gestation lasts about 6-8 weeks and the cubs are born between January and March, while the female is still in hibernation (Linnell *et al.*, 2000; Friebe, Swenson & Sandegren, 2001). In brown bears, a litter usually consists of one to three cubs (Steyaert *et al.*, 2012). Mass of the newborn cubs is up to 500 g, and at this stage the neonates are highly dependent on lactation and maternal care (Swenson *et al.*, 2000). Males do not provide parental care (Dahle & Swenson, 2003a). In slow-reproducing species such as brown bears, infanticide (killing of offspring by males) often occurs as an adaptive male strategy to force females into estrus (Steyaert *et al.*, 2012). As infanticide can significantly affect the reproductive success of females, they have evolved different strategies, such as aggressive behavior (Steyaert *et al.*, 2012), spatio-temporal avoidance of adult males (Dahle & Swenson, 2003a; Rode, Farley & Robbins, 2006), or disguised paternity by mating with several males (Bellmain et al., 2006), to cope with this threat. Young bears usually stay with their mothers for 1.5 to 2.5 years, after which mother wean them, and reenter a new reproductive cycle (Dahle & Swenson, 2003b; Tosoni *et al.*, 2017). After being weaned from their mothers, young bears disperse to avoid inbreeding, (Zedrosser *et al.*, 2007b). Despite the fact that natal dispersal is observed in both males and females, males are more prone to this behavior compared to the more philopatric females (Støen *et al.*, 2006; Zedrosser *et al.*, 2007b).

2.3.2. Hibernation in brown bears

Brown bears are facultative hibernators in which hibernation occurs as a strategy to cope with severe and adverse environmental conditions and food shortage during winter (Krofel, Špacapan & Jerina, 2017). The hibernation period is preceded by hyperphagia, during which bears accumulate fat reserves which are used as energy to survive the upcoming hibernation (Swenson *et al.*, 2000; Naves *et al.*, 2006; T. Robbins *et al.*, 2007; Stenset *et al.*, 2016). Brown bears usually hibernate in a den such as natural caves, tree cavities, or self-dug dens (González-Bernardo *et al.*, 2020), and while in a den, they do not eat, drink, nor urinate or defecate (Linnell *et al.*, 2000). Compared to small hibernating species (Nelson & Robbins, 2015), their body temperature drops only slightly (~4°C; Hellgren, 1998; Evans *et al.*, 2016; González-Bernardo *et al.*, 2020). Although the main drivers of hibernation in bears are not yet fully understood, previous research suggests a complex interaction

between both environmental (snow cover, ambient temperature, food availability) and internal factors (age, sex, reproductive status, condition, etc.) (Manchi & Swenson, 2005; Evans *et al.*, 2016; Krofel *et al.*, 2017; Bojarska *et al.*, 2019). Depending on the severity of the winter, hibernation lasts from 1.5 months for bears in southern regions to 7 months for their northern counterparts (Manchi & Swenson, 2005; Kaczensky *et al.*, 2006; Nores *et al.*, 2010; Graham & Stenhouse, 2014). Remaining active during winter has been observed in brown bears (particularly in males), and it is mostly associated with mild weather conditions or prolonged food availability during winter (Van Daele, Barnes & Smith, 1990; Huber & Roth, 1997; Nores *et al.*, 2010). Furthermore, brown bear hibernation phenology varies significantly depending on the age and reproductive status of the individual. Given that female give birth during hibernation, females with offspring spent significantly more time in the winter den, compared to solitary females and males (Friebe *et al.*, 2001; Haroldson *et al.*, 2002; Manchi & Swenson, 2005; Krofel *et al.*, 2017; González-Bernardo *et al.*, 2020).

2.4.   Brown bear feeding habits

Although they belong to the order Carnivora, brown bears are opportunistic omnivores, with the diet of some populations being predominantly plant-based (Robbins, Schwartz & Felicetti, 2004; Naves *et al.*, 2006; Bojarska & Selva, 2012). As an adaptation, their digestive tract is slightly longer compared to other carnivores, allowing them to digest plant material better (Swenson *et al.*, 2000). During the active period of the year, bears exhibit remarkable variations in food intake. After emerging from hibernation in spring, bears generally do not spend much time foraging (hypophagia), but rather use their energy to search for a mating partner (Swenson *et al.*, 2000; Steyaert *et al.*, 2012). In summer, food intake increases and ends with a hyperphagia period in the autumn, during which bears spend most of their time feeding or searching for food (Swenson *et al.*, 2000). During spring hypophagia, bears rely mainly on green vegetation and insects such as ants and bees, while during hyperphagia they concentrate on consuming energy-rich food such as overripe fruit (pears, plums, apples but also wild berries) or hard masts (acorns, beechnuts, chestnuts) (Swenson *et al.*, 1999a, 2000; Naves *et al.*, 2006; Bojarska & Selva, 2012). However, due to the different food availability, considerable differences in bears' diet can be observed depending on the geographical area they inhabit. In general, bears inhabiting northern Europe rely more on wild berries such as bilberry (*Vaccinium myrtillus*), crowberry (*Empetrum nigrum* and *Empetrum hermaphoditum*), lingonberry (*Vaccinium vitis-idaea*) during hyperphagia; Persson *et al.*, 2001; Stenset *et al.*, 2016), due to the lack of hard masts (acorns, beechnuts, and hazelnuts) which are very common in the diet of southern populations (Bojarska & Selva, 2012). Furthermore, in areas where bears have access to spawning salmon streams, such as in Alaska or on the Pacific coast or Russia, fishing is an important strategy to ensure a high protein intake (Van Daele *et al.*, 2013; Seryodkin, Panichev & Slaght, 2016; Sorum, Joly & Cameron, 2019).

2.5.   Brown bear movement and diel activity behavior

Brown bears are solitary animals that occupy large, overlapping home ranges. Bears are generally considered non-territorial animals (Dahle & Swenson, 2003c; Bellemain *et al.*, 2006), with males having three to four times larger home ranges than females (Mcloughlin, Ferguson & Messier, 2000). Therefore, it is not surprising that home ranges of several

females may overlap with one male home range (Mcloughlin *et al.*, 2000; Støen *et al.*, 2005), even though male ranges can also overlap (Huber & Roth, 1993). In addition to sex differences, the size of a bear's home range is also influenced by many other factors such as age, reproductive status, population density or food availability (Dahle & Swenson, 2003c; De Angelis *et al.*, 2021). Furthermore, significant differences have been observed regarding the activity patterns of brown bears living in different geographical areas. Compared to brown bears from North America, which are predominantly diurnal (Munro *et al.*, 2006), their European counterparts are more active during the night and crepuscular hours (Kaczensky *et al.*, 2006; Ordiz *et al.*, 2014; Parres *et al.*, 2020), which can also vary depending on the season, age and reproductive status of the bears. For example, females with dependent offspring often modify their movements and become more diurnal in order to avoid infanticide (Steyaert *et al.*, 2012; Steyaert, Swenson & Zedrosser, 2014b).

3. Human disturbance, management practices and climate change alter brown bear behavior and life history

Given their widespread distribution, brown bears are an interesting model species for understanding the impact that the expansion of human activities (Figure 4) and associated global warming may have on mammalian movements and life histories. This knowledge is crucial for the development of future conservation and management strategies for bears inhabiting human-modified environments.
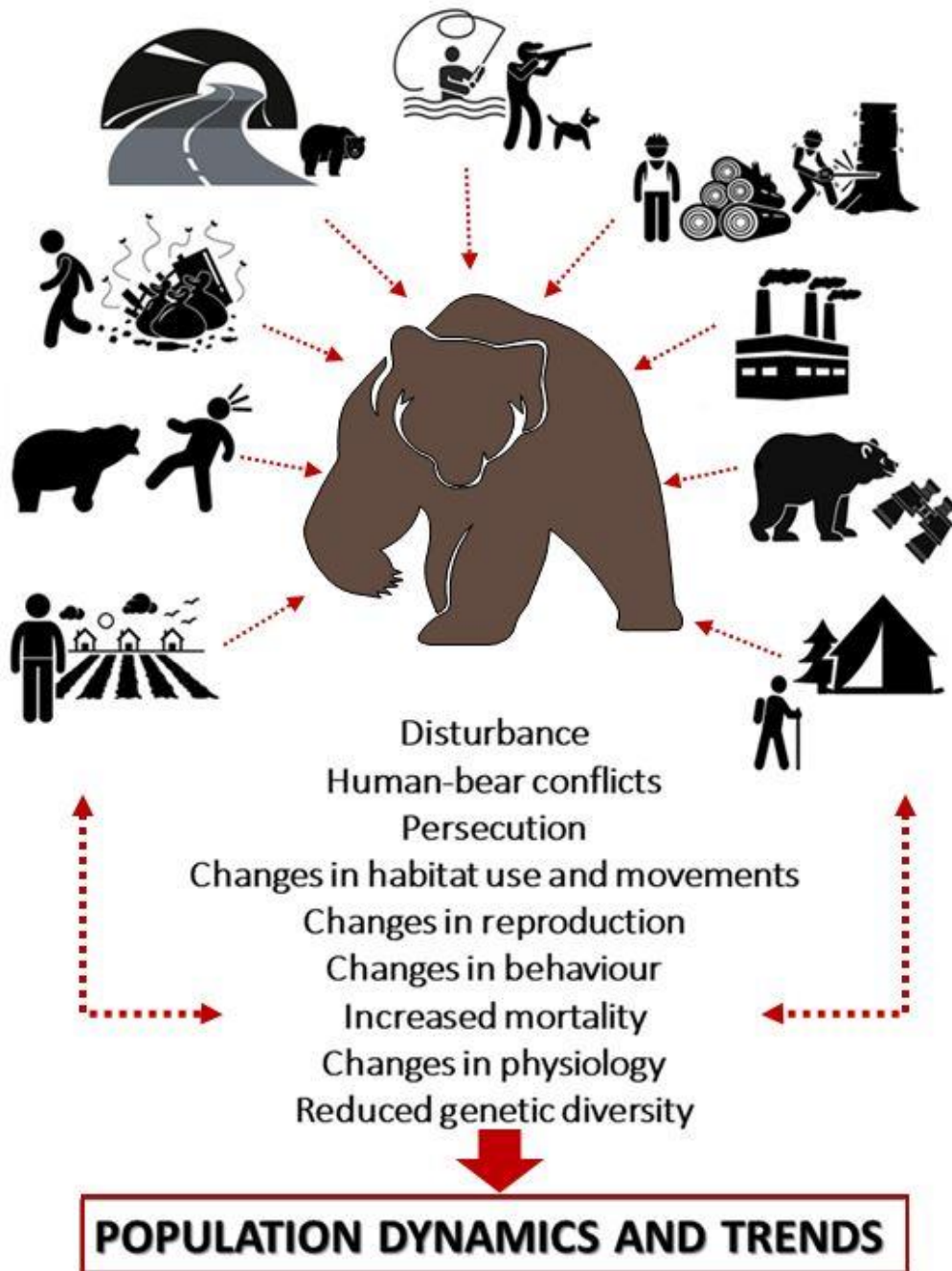

Figure 4. The most important human-related factors threatening brown bears worldwide (adapted from Morales-González *et al.*, 2020)

3.1. Effects of humans

3.1.1. Human-caused habitat modification and associated disturbance

Human encroachment into brown bear habitat is now greater than ever, and it will continue to increase, especially in Europe. However, there is evidence that bear populations are recovering and recolonizing their former range (Chapron *et al.*, 2014). Even though brown bears are very cautious around humans, it is not possible to completely avoid encounters with humans in human-dominated landscapes. Therefore, brown bears have undergone significant behavioral adjustments that have enabled them to coexist with humans in a shared landscape. Changes in spatio-temporal space use and movement patterns are often seen as the most common responses to human-caused habitat modifications (Martin *et al.*, 2010; Ordiz *et al.*, 2011, 2014, 2017, 2021; Penteriani *et al.*, 2018; Zarzo-Arias *et al.*, 2018; Parres *et al.*, 2020; De Angelis *et al.*, 2021). In general, it has been shown that nocturnal activity in European brown bears has probably developed as a strategy to avoid encounters with humans in densely populated landscapes (Kaczensky *et al.*, 2006; Martin *et al.*, 2010; Ordiz *et al.*, 2014). While bears generally avoid humans on a landscape and home range scale, studies suggest that females with dependent offspring might approach human settlements to avoid male bears (Steyaert *et al.*, 2016a). This "human shield" hypothesis suggests that some individuals use areas disturbed by humans to avoid conspecifics. By exhibiting tolerance towards humans, these individuals may reduce the risk of predation and sexually selected infanticide and increase the survival probability of their offspring (Nellemann *et al.*, 2007; Elfström *et al.*, 2014; Steyaert *et al.*, 2016a). Generally, in areas where human-modified landscapes overlap with bears' preferred habitats, bears often select for higher and more rugged terrains that are less accessible to humans (Nellemann *et al.*, 2007; Martin *et al.*, 2010; Steyaert *et al.*, 2016b; Skuban *et al.*, 2017; Penteriani *et al.*, 2018; Zarzo-Arias *et al.*, 2019). However, some individuals may be attracted to human settlements due to the presence of reliable food sources, which in turn could increase human-bear conflicts and the risk of being killed (Northrup, Stenhouse & Boyce, 2012b; Lamb *et al.*, 2017; Penteriani *et al.*, 2018). Furthermore, human infrastructure such as roads or railways has been shown to be a major cause of mortality in some populations (Nielsen, Stenhouse & Boyce, 2006; Northrup *et al.*, 2012a; Boulanger, Stenhouse & Margalida, 2014; McLellan, 2015; Penteriani *et al.*, 2018). As brown bears have large spatial requirements, they are also particularly vulnerable to the lack of continuous suitable habitats (Nellemann *et al.*, 2007; de Gabriel Hernando *et al.*, 2021). There is increasing evidence that habitat fragmentation caused by land-use change and intensive road infrastructure development will seriously affect the viability of brown bear populations in the future (Northrup *et al.*, 2012a, 2012b; Mateo-Sánchez *et al.*, 2014; Steyaert *et al.*, 2016a; Skuban *et al.*, 2017; Penteriani *et al.*, 2018). In addition, forestry can have a strong impact on bears, mainly by altering their foraging behavior (Frąckowiak *et al.*, 2014), but also the abundance of food resources (Hertel *et al.*, 2016a). In particular, clearing the forest allows more light to reach the forest floor, leading to high berry production, at least in the first year, which has been shown to be particularly important for bears during hyperphagia (Hertel *et al.*, 2016a). Furthermore, industrial activities, through changing habitat quality due to pollution, noise and accompanying human disturbance, threaten bear populations worldwide by transforming their habitats into less favorable or even hostile environments (Linke *et al.*, 2005; McLellan, 2015; Richardson, 2017).

In addition, human recreational activities such as hiking, biking, skiing, camping, etc. are often perceived as stressful by bears and can severely reduce their movement and foraging efficiency as well as their reproductive success and ultimately affect their survival (Nellemann *et al.*, 2007; Fortin *et al.*, 2016; Morales-González *et al.*, 2020). In addition, brown bear observation programs have become common practice in many countries, and in some areas they are even associated with bear feeding stations (Penteriani *et al.*, 2017). Considering that this practice usually takes place in areas that bears use for mating, feeding or rearing their cubs, increased disturbance by humans could cause bears to change their activity patterns or even leave such areas (Rode *et al.*, 2007; Fortin *et al.*, 2016; Penteriani *et al.*, 2017).

3.1.2. Supplementary feeding

Intentional provisioning of food to animals (i.e. supplementary feeding) is a common practice in many countries (Oro *et al.*, 2013; Cozzi *et al.*, 2016; Selva *et al.*, 2017; Penteriani *et al.*, 2021). It is mostly used as a game management tool, although some scientists emphasize its importance for population recovery programs, research purposes and even to divert bears from human settlements (i.e. diversionary feeding) (Selva *et al.*, 2014, 2017; Steyaert *et al.*, 2014a; Kavčič *et al.*, 2015; Penteriani *et al.*, 2018). Even though this field is just beginning to be investigated, many researchers have raised concerns about the potential negative impact that these food subsidies could have on a variety of species. Given their opportunistic diet and high nutritional requirements, bears are highly susceptible to this spatio-temporally predictable food source, which has been shown to affect many aspects of the brown bears' life cycle including their feeding behavior, movement patterns, timing of activity, space use, intraspecific interactions and hibernation (Kavčič *et al.*, 2015; Cozzi *et al.*, 2016; Štofík *et al.*, 2016; Krofel *et al.*, 2017; Selva *et al.*, 2017; Penteriani *et al.*, 2021). In general, in areas with access to supplemental food, bears may occupy smaller home ranges (Cozzi *et al.*, 2016; De Angelis *et al.*, 2021), change their movement patterns (Selva *et al.*, 2017; Penteriani *et al.*, 2018), habituate to humans (Kavčič *et al.*, 2015) or disrupt hibernation (Krofel *et al.*, 2017; Bojarska *et al.*, 2019). In addition, it has been shown that the reproductive behavior of brown bears can be affected by the presence of spatially clumped and predictable food resources (e.g. spawning salmon or garbage dumps; Craighead, Sumner & Mitchell, 1995; Steyaert *et al.*, 2012). In areas where artificial feeding of brown bears is common practice, bears may therefore begin to use such places as mating areas, thereby minimizing the amount of energy required to find mates.

In Serbia, brown bears are subject to supplementary feeding at several sites within their habitats, which is aimed to reduce damage, but also to help the brown bear population recover (Ćirović & Paunović, 2018). However, most of the existing feeding sites are primarily used as baiting sites for game management, especially for wild boar (*Sus scrofa*). According to our camera trap data, these supplementary feeding sites are frequently used by many wildlife species, including bears (*Ursus arctos*), wolves (*Canis lupus*), wild boars (*Sus scrofa*), foxes (*Vulpes vulpes*), badgers (*Meles meles*), etc. Depending on the location of the feeding site, grain food (usually corn) and carcasses (for feeding vultures or as wolf bait) are often provided to wildlife throughout the year, although data on the frequency and quantity of food provision has often not been systematically collected. Currently, it is estimated that due to the relatively high density of feeding sites, the amount of food (especially corn) provided to wildlife reaches more than 1000 tons per year (unpublished

data). Furthermore, in addition to a large number of registered feeding sites, a significant amount of grain food ends up deposited for wild boar baiting at numerous unregistered sites, which are frequently visited by other non-target species, including bears.

3.1.3. Hunting

Through their common history, the human-bear relationship has always been challenging, as bears often cause crop damage, kill livestock or sometimes even attack or kill humans (Penteriani *et al.*, 2016, 2018; Zarzo-Arias *et al.*, 2018). Therefore, bear hunting has been legalized in several countries as a way to remove nuisance individuals, increase societal acceptance of bears or control the size of bear population (Ordiz *et al.*, 2012; Penteriani *et al.*, 2018; Morales-González *et al.*, 2020). However, hunting has been shown to be associated with several negative effects, especially when harvest rates are too high (Morales-González *et al.*, 2020). A long history of persecution, particularly in Europe, has led to significant behavioral changes in brown bears. Individuals become more nocturnal during the hunting season in order to reduce the probability of being shot by diurnal hunters (Swenson, 1999; Ordiz *et al.*, 2012; Hertel *et al.*, 2016b). Hunting has also been shown to affect dispersal behavior of brown bears, as the removal of dominant males leaves empty territories that young individuals can easily occupy (Frank *et al.*, 2017). In addition, high hunting pressure during the hyperphagia season can significantly reduce foraging success and force bears to roam over wider and less suitable areas (Ordiz *et al.*, 2012; Hertel *et al.*, 2016b). Furthermore, as hunting of bear family groups is prohibited, long-term hunting pressure might prolong maternal care over time if females with longer maternal care have a higher survival probability and if length of maternal care is a heritable trait (Zedrosser *et al.*, 2011; Bischof *et al.*, 2018; Van De Walle *et al.*, 2018). Despite the beneficial effects that hunting can have on preventing human-bear conflict, this leisure activity is associated with population declines, lower reproductive success and altered demographic structure in all hunted bear populations (Bischof *et al.*, 2009; Zedrosser *et al.*, 2011; Gosselin *et al.*, 2014; Frank *et al.*, 2017).

3.2. Effects of climate change

Global climate change is now more pronounced than ever, and these changes are expected to be even more pronounced in the future. As bears are hibernators, there is intense debate about how a changing climate, together with immense anthropogenic pressure on natural habitats, will alter the winter behavior of the species (Friebe *et al.*, 2014; Pigeon, Stenhouse & Côté, 2016; Krofel *et al.*, 2017; Bojarska *et al.*, 2019). Previous research has shown that ongoing climate change which results in milder winters (Jacob *et al.*, 2014) will inevitably alter bear' winter behavior causing bears to shorten or even forgo hibernation (Evans *et al.*, 2016; Bojarska *et al.*, 2019; González-Bernardo *et al.*, 2020). Furthermore, there is increasing evidence that prolonged food availability together with supplementary feeding practices can disrupt hibernation in bears, leading to a delay in the onset of hibernation, frequent interruptions or a shortening of hibernation (Van Daele *et al.*, 1990; Nores *et al.*, 2010; Krofel *et al.*, 2017; Selva *et al.*, 2017; Bojarska *et al.*, 2019). Climate warming will inevitably affect the reproductive behavior of brown bears, especially in females, as they give birth during the winter period. As winters become milder (Jacob *et al.*, 2014), the energetic costs of hibernation will increase, leading to fewer energy reserves that can be

invested in reproduction (Humphries, Thomas & Speakman, 2002; Albrecht *et al.*, 2017). Furthermore, earlier exit of females with cubs from the den could jeopardize the offspring survival and thus reduce fitness (Pigeon *et al.*, 2016; Hertel *et al.*, 2018). In addition, a changing climate could strongly influence the feeding behavior of bears. In fact, changes in vegetation phenology (i.e. timing and intensity of ripening) are expected to lead to a mismatch between food availability and bear phenology (Roberts, Nielsen & Stenhouse, 2014; Hertel *et al.*, 2018; Penteriani *et al.*, 2019).

II SUBJECT OF THE DOCTORAL DISSERTATION

The main subject of the doctoral dissertation is the study of spatio-temporal movement patterns of brown bears (*Ursus arctos*) in the Central Balkans with the identification of the most important factors influencing these patterns.

The main objectives of this study are:

1. Analysis of movement patterns between different reproductive classes (adults, subadults and females with offspring) during the active period of the year (mating and hyperphagia season),

2. Analysis of activity and movement patterns, including den switching and the absence of denning behavior, during the winter months and describing factors influencing specific behavioral patterns,

3. Analysis of spatial and temporal movement patterns in relation to population and environmental variables (temperature, precipitation, snow cover, food availability, shelter availability, distance from settlements, type of vegetation, presence of artificial feeding station, number of tourists) which shape bear behavioral patterns.

III PAPERS RESULTING FROM THE DOCTORAL DISSERTATION

1. Seasonal and diel movement patterns of brown bears in a population in southeastern Europe

<div align="right">

Paper I

</div>

RESEARCH ARTICLE

Ecology and Evolution

WILEY

Seasonal and diel movement patterns of brown bears in a population in southeastern Europe

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Abstract

Most animals concentrate their movement into certain hours of the day depending on drivers such as photoperiod, ambient temperature, inter- or intraspecific competition, and predation risk. The main activity periods of many mammal species, especially in human-dominated landscapes, are commonly set at dusk, dawn, and during nighttime hours. Large carnivores, such as brown bears, often display great flexibility in diel movement patterns throughout their range, and even within populations, striking between individual differences in movement have been demonstrated. Here, we evaluated how seasonality and reproductive class affected diel movement patterns of brown bears of the Dinaric-Pindos and Carpathian bear populations in Serbia. We analyzed the movement distances and general probability of movement of 13 brown bears (8 males and 5 females) equipped with GPS collars and monitored over 1–3 years. Our analyses revealed that movement distances and probability of bear movement differed between seasons (mating versus hyperphagia) and reproductive classes. Adult males, solitary females, and subadult males showed a crepuscular movement pattern. Compared with other reproductive classes, females with offspring were moving significantly less during crepuscular hours and during the night, particularly during the mating season, suggesting temporal niche partitioning among different reproductive classes. Adult males, solitary females, and in particular subadult males traveled greater hourly distances during the mating season in May-June than the hyperphagia in July–October. Subadult males significantly decreased their movement from the mating season to hyperphagia, whereas females with offspring exhibited an opposite pattern with almost doubling their movement from the mating

to hyperphagia season. Our results provide insights into how seasonality and reproductive class drive intrapopulation differences in movement distances and probability of movement in a recovering, to date little studied, brown bear population in southeastern Europe.

KEYWORDS

brown bear, movement patterns, Serbia, *Ursus arctos*

1 | INTRODUCTION

The diel and seasonal movement patterns of mammals are shaped by a suite of environmental drivers, among them photoperiod (Nielsen, 1983), temperature (Pigeon et al., 2016; Seryodkin et al., 2013), food availability (Heurich et al., 2014; Klinka & Reimchen, 2009), and inter- and intraspecific competition (Monterroso et al., 2013), although seasonal variation in human activity (Gaynor et al., 2018; Marchand et al., 2014) can further modify these patterns. The rapid growth of human populations has forced many wild animals to share their living space with humans, in the so-called human-dominated landscapes (Gaynor et al., 2018; Zarzo-Arias et al., 2018). Under such conditions, the possibility of human–wildlife encounters increases significantly, which is why many animals, in order to avoid potential encounters, shift their movement to times when human activity is low (Brook et al., 2012; Gaynor et al., 2018; Ordiz et al., 2014). For carnivores, significant shifts in diel activity toward the dark and crepuscular hours of the day have been observed in human-dominated landscapes (Gaynor et al., 2018; Wu et al., 2018), which is considered to be a consequence of anthropogenic stress (Seryodkin et al., 2013).

The brown bear (*Ursus arctos*) is a large carnivore that inhabits human-dominated landscapes in Europe (Chapron et al., 2014; Swenson et al., 1999; Zedrosser et al., 2001). Bears show natural variation in movement patterns over the course of the year as a result of their life history, which includes three important stages, that is, mating, hyperphagia, and hibernation (Swenson et al., 2000). Additionally, intraspecific interactions (both attraction and avoidance) are important factors for shaping bear behavior, leading to variations between different reproductive classes (Kaczensky et al., 2006; Lewis & Rachlow, 2011). During the mating season, which usually occurs in the late spring/early summer, movement patterns of adult bears are predominantly shaped by reproductive behavior, that is, the search and courting of partners (Dahle & Swenson, 2003; Steyaert et al., 2012). Adult females with dependent cubs of the year try to avoid adult males during this time period to avoid infanticide (Steyaert et al., 2013, 2014; Swenson et al., 2003), whereas subadults modify their behavior as a result of natal dispersal (Zedrosser et al., 2007). During the hyperphagia season in summer and autumn, movement of all reproductive classes is mostly driven by food search to increase adipose tissue in preparation for hibernation.

Although natural food resources are often widely dispersed (Hertel, Steyaert, et al., 2016), artificial feeding sites can provide a clumped, high-calorie food sources which can alter bear movement patterns (Kavčič et al., 2013; Selva et al., 2017; Ziegltrum & Nolte, 1997). Also, humans greatly affect bear behavior and life history (Hertel, Zedrosser, et al., 2016; Ordiz et al., 2014; Van de Walle et al., 2018; Zedrosser et al., 2011), and bears generally try to avoid humans on a spatio-temporal scale, that is, bears move mostly during night and crepuscular hours when human activity on the landscape is lower (Kaczensky et al., 2006; Ordiz et al., 2014; Parres et al., 2020; Roth, 1980; Roth & Huber, 1986). Therefore, sustainable bear conservation and management must take into consideration the natural patterns of bear movement as well as the behavioral responses to human disturbance (Hertel et al., 2017; Tuomainen & Candolin, 2011; Zarzo-Arias et al., 2018).

Brown bears in Serbia are at the interface of the Dinaric-Pindos and the Carpathian populations and, thus, represent a potential connection for genetic exchange between these two large populations in southeastern Europe (Ćirović et al., 2015). This makes bears in Serbia of particular conservation concern, which in combination with increasing human impact on brown bear habitats and their strictly protected status (Ćirović & Paunović, 2018), requires the application of well-planned conservation actions. Here, we carry out a systematic analysis of bear diel movement patterns in Serbia, with the goal to improve future bear management and conservation.

The main aim of this study was to evaluate the differences in seasonal and diel movement patterns for different reproductive classes of brown bears in a human-dominated landscape and area of great conservation concern. Based on existing literature of diel movement patterns of brown bears in human-dominated landscapes (Ćirović et al., 2015; Hertel et al., 2017; Kaczensky et al., 2006; Parres et al., 2020), we predicted (i) that bears would follow a bimodal movement pattern with periods of high movement during crepuscular hours and that (ii) bears would move over longer distances during the mating than during the hyperphagia season. We further predicted that (iii) dispersing subadult males would travel longer distances during the mating season than adults and females with dependent offspring and that (iv) differences in movement patterns between reproductive classes would be less pronounced during the hyperphagia than during the mating season.

2 | MATERIALS AND METHODS

2.1 | Study areas and bear capture

Bears were monitored in two study areas in Serbia, the Stari Vlah-Raška Mountain Range (~43°50′, 19°27′), which is part of the Dinaric-Alps in southwestern Serbia, as well as on Južni Kučaj Mountain (~44°05′, 21°50′), which is part of the Carpathian Mountain Range in eastern Serbia (Figure 1). There is no connection between these two populations (Ćirović & Paunović, 2018). The Stari Vlah-Raška Mountain Range has altitudes ranging from 750 to 1500 m above sea level (Pavlović et al., 2017), and ~35% of the area (240,000 ha) is covered with dense forests dominated by silver fir (*Abies alba*), Norway spruce (*Picea abies*), and beech (*Fagus* spp.). The rest of the landscape is covered with agricultural land, such as pastures, meadows, and orchards. (Pavlović & Živković, 2003). The bear population in southwestern Serbia, with an estimated population size of 60 ± 10 bears and a slightly increasing population trend, is considered part of the large Dinaric-Pindos population (Chapron et al., 2014; Kaczensky et al., 2013). Južni Kučaj Mountain (max. elevation 1284 m) is mostly covered by beech and beech–coniferous forests (72% of the area), and agricultural land covers the remaining 29%. The bear population in eastern Serbia is very small (~6 individuals) but is considered part of the large Carpathian bear population (Chapron et al., 2014; Kaczensky et al., 2013). The only monitored bear from this population was a female that had been translocated from the Dinaric-Pindos population in western Serbia in 2007. Bear populations in both areas have access to a network of supplementary feeding sites for ungulates as well as diversionary feeding sites used to prevent bears from searching for food near humans.

We captured bears using Aldrich foothold snares (Johnson & Pelton, 1980) in the time period 2007–2019. Bears were chemically immobilized with an intramuscular injection of 3 ml tiletamine–zolazepam (Zoletil 100; Virbac, Prague, Czech Republic; initial vol 10 mg/kg) using a dart gun (Dan-Inject®, Børkop, Denmark). Standard body measurements were taken at each capture, and age was estimated based on body mass and size, as well as tooth wear (Jonkel,

1993; Karamanlidis et al., 2015). Each bear was equipped with a GPS collar with GSM download (GPS Plus; Vectronic Aerospace GmbH, Berlin, Germany) and a timer-controlled drop-off system. Bears were released at the trap site (Ćirović et al., 2015), with the exception of one adult female, which was translocated for management reasons from the Stari Vlah-Raška Range to Južni Kučaj in 2007. All GPS collars were scheduled to record a location every 1 h (24 positions/day). The GPS relocation success rate during the active period ranged from 65 to 97% (mean: 84%). Permit for the capture and handling brown bears was provided by the Ministry of Environmental Protection (license number: 353-01-1053/2019-04).

2.2 | GPS data, intensity, and probability of movement

We analyzed diel movement patterns for 8 males and 5 females followed over 1–3 years (i.e., "bearyear"—each year during which a bear was monitored) (Table 1). GPS-collared brown bears were grouped according to their sex and age into subadults (<5 years) and adults (≥5 years) (Dahle & Swenson, 2003; Elfström & Swenson, 2009). Females were further distinguished by their reproductive status as being accompanied by offspring or being solitary. This led to four categories: adult males (nBearyear = 8), subadult males (nBearyear = 6), solitary females (nBearyear = 8), and females with dependent offspring (nBearyear = 4) (Hertel et al., 2017; Ordiz et al., 2007; Steyaert et al., 2013; Table 1).

Bears in southeastern Europe hibernate approximately from the end of November until the end of March (Kaczensky et al., 2006). We divided the active period of the year (from May 1 until October 31, i.e., outside of the hibernation period) into two distinct seasons: the mating season, which lasts 2 months in spring and early summer (defined here as May 1–June 30), and hyperphagia season, which occurs after mating is completed until hibernation in autumn (defined as July 1–October 31) (Ciucci et al., 2014; Steyaert et al., 2013). We excluded the months of April and November from the analysis due to the very low number of locations (some bears may not have
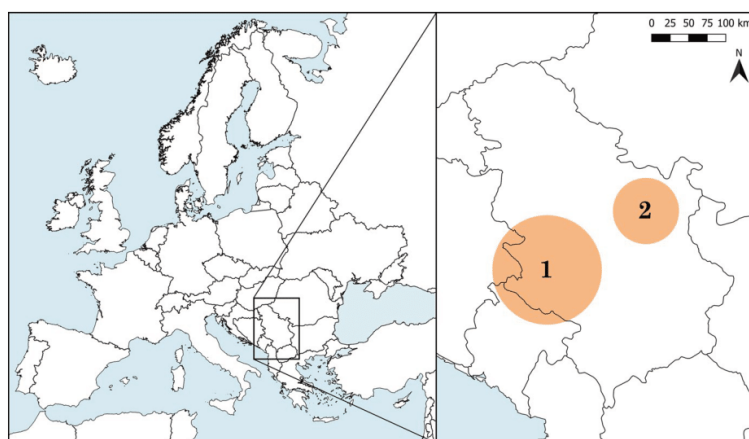

FIGURE 1 Location of study areas for seasonal and diel activity patterns of brown bears in Serbia, 2007–2019; (1) Stari Vlah-Raška Mountain Range, (2) Južni Kučaj Mountain

TABLE 1 Data used in the analysis of movement patterns of brown bears in Serbia, 2007–2019

Reproductive class	Bear ID	Study area	Observation days used in analysis	Number of bearyears
Adult males	Batica	Stari Vlah	129	2
	Dobrivoje	Stari Vlah	181	1
	Ogi	Stari Vlah	366	2
	Rača	Stari Vlah	260	2
Subadult males	Andrej	Stari Vlah	96	2
	Miloje	Stari Vlah	183	1
	Miloš–2019 (adult)	Stari Vlah	372	3
	Zoran	Stari Vlah	68	1
Solitary females	Milica	Južni Kučaj	374	3
	Sonja	Stari Vlah	332	2
Females with dependent offspring	Flekica	Stari Vlah	336	2
	Medena	Stari Vlah	219	2
	Slobodanka	Stari Vlah	464	3

TABLE 2 Candidate models to explain the temporal trends in movement distance and probability of movement of brown bears in Serbia, 2007–2019, in relation to reproductive class (adult male, subadult male, solitary female, and female with dependent offspring), that is, bearclass model and season (mating and hyperphagia season), that is, seasonal model

	Explanation
Bearclass model	
Movement distance/probability of movement ~s(hour, by=reproductive class) + reproductive class	s(hour, by = reproductive class) denotes the differences in the movement distance and probability of movement between the reproductive classes at different hours of the day, and "reproductive class" denotes the general differences in movement and probability of movement between the reproductive classes
Movement distance/probability of movement ~s(hour, by = reproductive class)	s(hour, by = reproductive class) denotes the differences in the movement distance and probability of movement between the reproductive classes at different hours of the day
Seasonal model	
Movement distance/probability of movement ~s(hour, by = season) + season	s(hour, by = season) denotes the differences in the movement distance and probability of movement between the seasons at different hours of the day, and "season" denotes the general differences in movement and probability of movement between seasons
Movement distance/probability of movement ~s(hour, by = season)	s(hour, by = season) denotes the differences in the movement distance and probability of movement between the seasons at different hours of the day

Note: Reproductive class = factor with four levels (the adult males, subadult males, single females, females with dependent offspring), season = factor with two levels (mating season, hyperphagia season). The interaction term "by" in the respective first models allows that the effect of hour of the day on the response variable differs between factor levels.

emerged from hibernation or have already entered the den). We extracted sunrise, sunset, and day length for every day in the mating and hyperphagia seasons for Central European Time (UTC + 1) and Central European Summer Time (UTC + 2) with the library *maptools* (Bivand & Lewin-Koh, 2014) using N 43°82" and E 19°72" (the village Tripkova, Zlatibor Mountain, Serbia) as reference coordinates. We further extracted civil dusk and dawn, that is, the time of day when the sun is between 6 and 0 degrees below the horizon (Ensing et al., 2014). The crepuscular hours of the day were defined as the time period between civil dawn until sunrise (morning twilight) and

from sunset until the end of civil dusk (evening twilight), and periods between sunrise and sunset and civil dusk and dawn were defined as day and night, respectively.

2.3 | Movement metrics

To describe bear movement patterns, we calculated two complementary metrics: (a) hourly movement distance, that is, meters/h and (b) probability of movement, a binary metric of whether a bear

moved (>50 m) or was stationary (<50 m) during a given hour of a day. We first calculated hourly movement distance as a measure of intensity of movement, that is, how much do bears move during any given hour of 24-h period. We then constructed regular movement trajectories for every bearyear, using the library _adehabitatLT_ (Calenge, 2006). Hourly movement distances were extracted from the trajectories as the Euclidean distance between two successive hourly locations. To avoid erroneous distance calculations (i.e., displacements over two hours or longer), all missing locations were set to NA, resulting in the removal of distance calculations one hour before and after a missing location (Hertel, Steyaert, et al., 2016). We further calculated the probability of movement by categorizing hourly movement distances into moving and stationary positions. Bears were considered stationary when the distance between two successive hourly locations was ≤50 m (coded as 0's), that is, two times the average GPS positional error (25 m) (Ćirović et al., 2015), whereas all movement distances >50 m (coded as 1's) were defined as moving positions.

2.4 | Statistical methods

We used generalized additive mixed models (GAMMs) to test for temporal trends in the movement distance and probability of movement during the course of 24 h by fitting a cyclic cubic spline over hour of day. In addition, we tested for temporal differences among reproductive classes (adult males, subadult males, solitary females, and females with dependent offspring) and seasons (mating and hyperphagia).

Hourly movement distance (in meters), that is, intensity of movement, was modeled as GAMM with a Gaussian distribution using the mgcv package (Wood, 2011). We used diagnostic plots to validate that the distribution of the residuals was normal and homogeneous. To improve model fit, we refitted models with a log-transformed response variable. We back-transformed model predictions to the original scale (meters) for better model interpretation.

Probability of movement was modeled as a binary response variable: moving (1) versus stationary (0) hourly intervals in a GAMM with a binomial distribution using the R package gamm4 (Wood & Scheipl, 2013). Hence, the model-predicted ratio between stationary and moving increments at any hour of the day represents a probability of movement (i.e., when bears move versus not move). We controlled for consistent among-individual differences in movement distance and probability of movement with a random intercept for Bearyear. We fitted two sets of models (Table 2): first, we tested whether diel movement patterns differed among reproductive classes by fitting a cyclic cubic spline over time of day interacting with reproductive class (bearclass model; Table 2). We fit this model separately for the mating and hyperphagia periods. Second, we tested whether diel movement patterns (for each reproductive class separately) differed among two seasons by fitting a cyclic cubic spline over time of day interacting with season (Seasonal model; Table 2). We used "by" function to include an interaction term in all

models. Because it was not possible to fit a three-way interaction (day, season, and reproductive class), we split our analyses into two model sets in order to interpret the contrast both among seasons but also among reproductive classes. We tested models against a simpler model not controlling for variation in the temporal trend among reproductive classes or seasons, respectively (Table 2). We selected the most parsimonious model based on second-order bias-corrected Akaike's information criterion (AIC), that is, models with an Akaike weight (AICcw) close to 1 receive most support relative to other candidate models (Tables S1 and S2) (Arnold, 2010). We validated model assumptions (normal distribution of residuals and absence of heteroscedasticity) by plotting residuals against fitted values. We controlled for inherent temporal autocorrelation in the movement data with the use of a spline over hour of the day and confirmed that no unmodeled temporal autocorrelation remained in the model (Figures S1 and S2).

Finally, we used generalized linear mixed models (GLMMs) to contrast differences in the probability of movement (binary response variable with moving versus stationary positions). We fitted principal periods of a day (factor with three levels: day, night, and crepuscular hours) as explanatory variables for each reproductive class (adult males, subadult males, single females, and females with dependent offspring) and season (mating versus hyperphagia) separately, using the package lme4 (Bates et al., 2014). The statistical software R 3.6.1 (R Development Core Team, 2019) was used in all analyses.

3 | RESULTS

We analyzed movement patterns of 13 brown bears monitored for 1–3 years (a total of 26 monitoring years, i.e., "bearyear"). During the active period of the year (May 1–October 31), individual bears were monitored for a minimum period of 20 days and a maximum of 184 days (mean monitoring period: 132 days).

3.1 | Movement distance

3.1.1 | Bearclass model

Movement distance was affected by the time of day and differed among reproductive classes during both the mating season (ΔAIC = −1767.5, AICcw = 1) and the hyperphagia season (ΔAIC = −904.1, AICcw = 1; Table S1).

During the mating season, movement distances for three out of four reproductive classes (adult males, subadult males, solitary females) were longest during the crepuscular hours before sunrise and after sunset and shortest during daytime, reaching their minimum level around noon (Figure 2, upper panel). Subadult males moved the longest hourly distances as compared with all other reproductive classes (~550 m, between 20:00–21:00 and 3:00–4:00; Figure 2 (upper left panel – light blue line); β = 4.63; Table 3). Solitary females and adult males moved significantly less during the same time

FIGURE 2 Predicted average hourly movement distances (upper panel) and predicted probability of movement within 24 h (lower panel) of 4 reproductive classes of brown bears (adult male, subadult male, solitary female, female with offspring) per season (mating: left panels, hyperphagia: right panels) in Serbia, 2007–2019. Vertical lines represent dawn, sunrise, sunset, and dusk, dividing a 24-h period into night (dark grey area), crepuscular hours (light grey area), and day (white area). Solid lines represent the maximum duration of the crepuscular period during both seasons, and dotted lines represent mean value
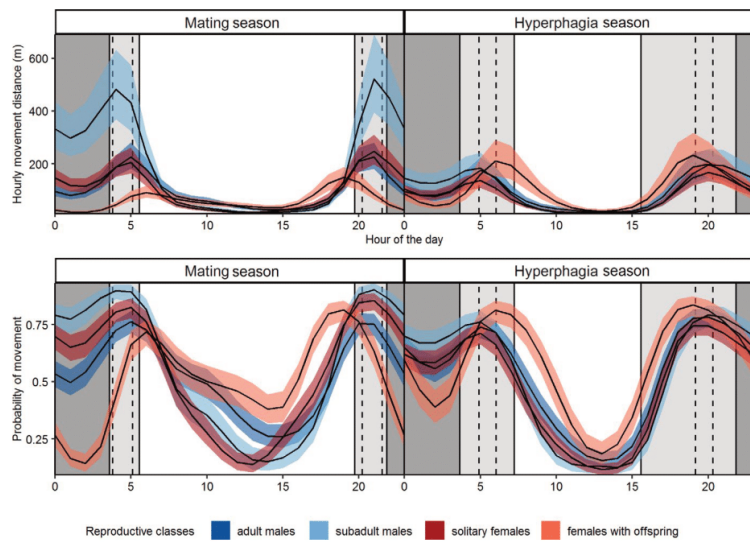
TABLE 3 Coefficients and standard errors ($\beta \pm$ SE) for the explanatory variable as well as the significance of the smoothing terms (edf, Chi.sq/F) obtained in the most parsimonious bearclass model predicting movement distance and probability of movement in the mating and hyperphagia period in relation to reproductive class of brown bears in Serbia, 2007–2019

		Mating period			Hyperphagia period	
Movement distance		β	SE		β	SE
	(Intercept)	4.63	0.12	(Intercept)	4.22	0.13
	Adult males	−0.25	0.15	Adult males	0.05	0.17
	Single females	−0.36	0.15	Single females	−0.17	0.17
	Females with offspring	−0.71	0.16	Females with offspring	0.20	0.20
		edf	F		edf	F
	Hour:subadult males	7.72	301.3	Hour:subadult males	7.74	413
	Hour:adult males	7.72	114.2	Hour:adult males	7.83	371
	Hour:single females	7.59	175.9	Hour:single females	7.84	604.2
	Hour:females with offspring	7.65	80.6	Hour:females with offspring	7.83	235.2
Probability of movement		β	SE		β	SE
	(Intercept)	0.45	0.14	(Intercept)	0.03	0.12
	Adult males	−0.31	0.17	Adult males	0.08	0.16
	Single females	−0.22	0.17	Single females	−0.12	0.16
	Females with offspring	−0.47	0.18	Females with offspring	0.32	0.19
		edf	Chi.sq		edf	Chi.sq
	Hour:subadult males	7.59	998.8	Hour:subadult males	7.59	1828
	Hour:adult males	7.57	490.3	Hour:adult males	7.72	1893
	Hour:single females	7.56	900.2	Hour:single females	7.77	2789
	Hour:females with offspring	7.74	643.3	Hour:females with offspring	7.77	1303

periods (~230 m; Figure 2, upper left panel – red and dark blue lines, respectively; $\beta_{\text{adult males}} = 4.38$ and $\beta_{\text{single females}} = 4.27$; Table 3). On the contrary, females with dependent offspring moved the longest hourly distances after sunrise (~100 m between 5:00–6:00) and before sunset (~180 m between 18:00–19:00; Figure 2 (upper left panel–orange line)) and moved significantly less during crepuscular hours and during night than the other reproductive classes (Figure 2, upper left panel – orange line).

In comparison to the mating season, the discrepancy in movement distances between reproductive classes was significantly less

pronounced during the hyperphagia season. Movement distances were longest during crepuscular hours and night for all reproductive classes, with females with dependent offspring showing a later peak in the morning and an earlier peak in the evening (Figure 2, upper right panel). During the hyperphagia season, females with dependent offspring traveled slightly longer hourly distances than the other three reproductive classes (~220 m between 18:00–19:00 and 5:00–6:00; Figure 2, upper right panel: orange line; $\beta_{\text{females with offspring}}$ = 4.44; Table 3), whereas solitary females moved the least during the same period (~150 m; Figure 2 (upper right panel - red line); $\beta_{\text{single females}}$ = 4.05; Table 3).

3.1.2 | Seasonal model

Movement distance in relation to time of the day differed among seasons for adult males (ΔAIC = −168.5, AICcw = 1), subadult males (ΔAIC = −282.3, AICcw = 1), solitary females (ΔAIC = −117.6, AICcw = 1), and females with offspring (ΔAIC = −619.7, AICcw = 1) (Table S2).

Adult males, solitary females, and in particular subadult males traveled greater distances during the mating season than during the hyperphagia season (Table 4, Figure 3, upper panel). Subadult males decreased their hourly movement distance from 463 m (between 20:00 and 21:00) in the mating season to 196 m during the same time period in the hyperphagia season (Figure 3, upper panel; $\beta_{\text{mating period}}$ = 4.49 and $\beta_{\text{hyperphagia period}}$ = 4.20; Table 4). Females with dependent offspring traveled shorter distances, that is, 92 m (between 5:00 and 6:00) during the mating season and increased their movement to 214 m for the same time periods during hyperphagia (Figure 3, upper panel; $\beta_{\text{mating period}}$ = 3.92 and $\beta_{\text{hyperphagia period}}$ = 4.42; Table 4).

3.2 | Probability of movement

3.2.1 | Bearclass model

The probability of movement was affected by the time of day and differed among reproductive classes during the mating (ΔAIC = −1389.7, AICcw = 1) and hyperphagia periods (ΔAIC = −581.4, AICcw = 1; Table S1). During the mating season, females with dependent offspring showed the highest probability for movement during day (59%) and crepuscular hours (57%) (β_{day} = 0.36 and $\beta_{\text{crepuscular}}$ = 0.26; Table 5), but their nocturnal movement level was low (24% probability of movement; β_{night} = −1.15; Table 5). Movement of adult males, subadult males, and solitary females occurred predominantly during crepuscular hours (75%, 93%, and 84%, respectively) and during night (56%, 81%, and 70%, respectively; Table 5).

During the hyperphagia season, probability of movement for all reproductive classes was highest during the crepuscular hours (Table 5). Adult males, subadult males, and solitary females were twice as likely to move during crepuscular hours (84%, 83%, 79%; Table 5) as during the day (40%, 32%, 35%; Table 5).

3.2.2 | Seasonal model

The probability of movement within 24 hours differed between seasons for adult males (ΔAIC = −186.5, AICcw = 1), subadult males (ΔAIC = −93.2, AICcw = 1), solitary females (ΔAIC = −85.6, AICcw = 1), and females with dependent offspring (ΔAIC = −408.6, AICcw = 1; Table S2). Adult males, subadult males and solitary females showed a slightly increased probability of movement during the mating season, compared with the hyperphagia season, whereas females with dependent offspring showed the opposite pattern, that is, slightly

TABLE 4 Coefficients and standard errors ($\beta \pm$ SE) for explanatory variable as well as significance of the smoothing terms (edf, Chi.sq/F) obtained in the most parsimonious seasonal model predicting movement distance and probability of movement for 4 reproductive classes of brown bears (adult male, subadult male, solitary female, female with dependent offspring) in relation to seasonal variation (mating and hyperphagia) in Serbia, 2007–2019

		Adult males		Females with offspring		Single females		Subadult males	
Movement distance		β	SE	β	SE	β	SE	β	SE
	(Intercept)	4.23	0.07	4.42	0.06	4.09	0.08	4.20	0.13
	Mating	0.12	0.03	−0.50	0.03	0.28	0.03	0.29	0.04
		edf	F	edf	F	edf	F	edf	F
	Hour:hyperphagia	7.81	322.8	7.84	257.9	7.85	616	8.76	353.4
	Hour:mating	7.69	106.9	7.69	94.6	7.64	193.4	8.75	274.4
Probability of movement		β	SE	β	SE	β	SE	β	SE
	(Intercept)	0.11	0.05	0.35	0.06	−0.03	0.07	0.01	0.15
	Mating	0.02	0.04	−0.37	0.04	0.35	0.04	0.26	0.06
		edf	Chi.sq	edf	Chi.sq	edf	Chi.sq	edf	Chi.sq
	Hour:hyperphagia	7.72	1890.7	7.77	1300.3	7.76	2768.5	7.59	1830
	Hour:mating	7.57	493.7	7.74	640.7	7.56	902.7	7.59	1004

FIGURE 3 Predicted average hourly movement distances (upper panel) and predicted probability of movement within 24-hour (lower panel) of brown bear reproductive classes (adult male, subadult male, solitary female, female with dependent offspring) during the mating (green line) and hyperphagia (orange line) seasons in Serbia, 2007–2019
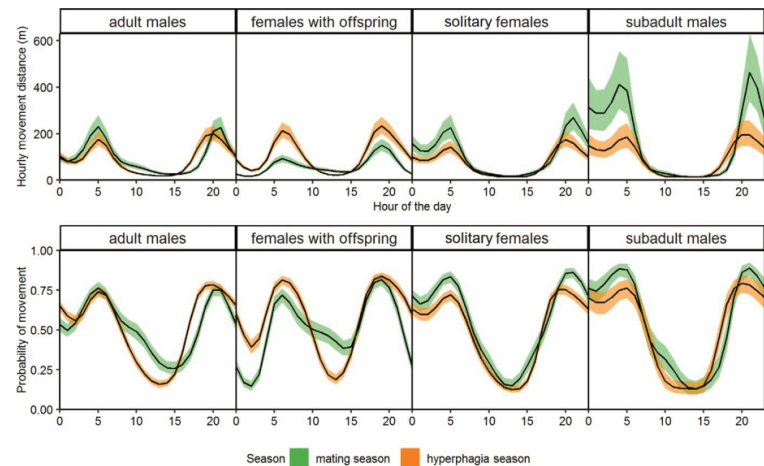
TABLE 5 Coefficients and standard errors ($\beta \pm$ SE) obtained in the generalized linear mixed model (GLMMs) predicting probability of movement for 4 reproductive classes of brown bears (adult male, subadult male, solitary female, female with dependent offspring) in relation to period of the day (day, night, crepuscular) during the mating and hyperphagia seasons in Serbia, 2007–2019

| | Adult males | | | | Females with offspring | | | |
| | Mating period | | Hyperphagia period | | Mating period | | Hyperphagia period | |
	β	SE	β	SE	β	SE	β	SE
(Intercept:day)	−0.08	0.06	−0.39	0.06	0.36	0.10	0.18	0.06
Night	0.31	0.06	0.94	0.04	−1.51	0.07	0.01	0.05
Twilight	1.18	0.10	2.08	0.08	−0.10	0.09	1.56	0.09
	Solitary females				Subadult males			
	Mating period		Hyperphagia period		Mating period		Hyperphagia period	
	β	SE	β	SE	β	SE	β	SE
(Intercept:day)	−0.20	0.16	−0.61	0.11	−0.29	0.16	−0.76	0.17
Night	1.07	0.07	1.09	0.03	1.77	0.09	1.63	0.05
Twilight	1.83	0.19	1.94	0.06	2.83	0.19	2.33	0.10

higher probability of movement level during hyperphagia (Table 4; Figure 3, lower panel). Females with dependent offspring change their probability of movement between mating (highest movement probability during daylight hours – 59%; β_{day} = 0.36; Table 5) and hyperphagia seasons (highest probability during crepuscular hours – 85%; $\beta_{crepuscular}$ = 1.74; Table 5). In addition, they almost doubled their probability of movement during night and crepuscular hours in the hyperphagia season (55% and 85%), compared with mating season (24% and 57%, respectively; Table 5).

4 | DISCUSSION

Our results generally support our predictions that diel movement patterns of brown bears in Serbia varied among different reproductive classes and between seasons. Based on our results, bears in our study area showed greatest movement rates during crepuscular and night hours, and lowest movement rates during diurnal time periods (support prediction i). In more detail, subadult males were mostly crepuscular, adult males, and solitary females were moving both during night and crepuscular hours with no pronounced resting period during the night, whereas females with offspring were moving more during daylight and crepuscular hours than other reproductive classes. This corresponds well with the findings of Moe et al. (2007) for Scandinavian female bears and with findings of Kaczensky et al. (2006) for adult brown bears in Slovenia and Croatia. Contrary to findings of Kaczensky et al. (2006) and Parres et al. (2020) that subadult bears are significantly more active during the day, and we found that subadult males in our study areas exhibited mostly crepuscular and nocturnal movement patterns during both the mating and hyperphagia periods and traveled greater distance than any other reproductive class during the dark hours of the mating season (support prediction) (iii). Nocturnality of younger individuals has also been observed in Scandinavian brown bears (Hertel et al., 2017).

This movement pattern probably represents a strategy to avoid encounters with crepuscular adult male bears and may reduce competition for food and space between these two classes.

However, the temporal niche partitioning observed in our study was less pronounced than other areas of the Dinaric-Pindos population (Kaczensky et al., 2006). This is likely related to the small population sizes in our study areas (~60 individuals in the Dinaric-Pindos and ~6 individuals in the Carpathian population) compared with Slovenia (~440 individuals) and Croatia (~1000 individuals) (Chapron et al., 2014; Kaczensky et al., 2013), that is, the relatively low population size may result in lower competition and reduced temporal niche partitioning compared with larger populations. In their study, Kaczensky et al. (2006) suggested that subadults are more day active to reduce food competition with nocturnal adults. Thus, the relatively small number of individuals in our study area and the resulting lower probability of encounters may explain why subadult bears are moving at similar times as other bear age and sex classes.

The generally higher movement rates of subadult males were likely related to natal dispersal (Zedrosser et al., 2007). Adult male and solitary female bears showed greater movement rates during the mating season than during the hyperphagia season (support prediction (ii), most likely due to mate search behavior. This assumption is supported by the results obtained by Dahle and Swenson (2003) who showed that both adult males and solitary females significantly decreased their ranges from mating to post-mating season (which overlaps with our definition of the hyperphagia season). Both classes had movement peaks at similar times of the day (Figure 2). A comparable pattern was also found in adult males and solitary females in the Pyrenean brown bear population during spring, which coincides with the mating season (Parres et al., 2020). Diurnal movement in adult bears in our study areas was very low during both seasons, which corresponds to the results obtained for adult bears in Slovenia and Croatia (Kaczensky et al., 2006).

All reproductive classes, except females with dependent offspring, decreased their movement rates from mating to the hyperphagia season (support prediction ii), with movement occurring mostly during night and crepuscular hours. Several studies have shown that bear activity is negatively affected by human presence (Hertel et al., 2017; Martin et al., 2010; Matthews et al., 2006; Nellemann et al., 2007). Parts of our study area are a popular tourist destination in Serbia, and the resulting human activity may be one of the reasons for the high degree of nocturnal movement of bears during both season; however, no data were available to test this effect.

Numerous previous studies of bear movement and activity patterns emphasize the impact of artificial feeding or baiting stations (intended either for bears and/or other wildlife) on bear movement patterns (Cozzi et al., 2016; Elfström et al., 2014; Fersterer et al., 2000; Jerina et al., 2013; Penteriani et al., 2017; Selva et al., 2017; Steyaert, Kindberg, et al., 2014). Although artificial feeding stations are present in our study area, due to insufficient data regarding their number, locations, and food supplementation frequencies for the entire monitoring period, we cannot evaluate their effect on bear movement rates. When feeding stations are present in a bears home range, we expect a reduced movement rate, in particular during the hyperphagia period because bears stay closer to the feeding stations. Future research should focus on the effect of feeding stations on bear movement patterns.

Females with dependent offspring showed a contrasting movement pattern compared with other reproductive classes, with movement occurring predominantly during daylight (mating season) and crepuscular hours (hyperphagia season). This is in line with other studies showing that females with offspring are more diurnal than other reproductive classes (Kaczensky et al., 2006; Munro et al., 2006; Parres et al., 2020; Rauer et al., 2003; Steyaert, Swenson, et al., 2014). During the mating season, adult males may kill cubs of the year (Steyaert, Swenson, et al., 2014), and females with cubs try to avoid infanticide by shifting their movement into daytime hours (Dahle & Swenson, 2003; Edwards et al., 2013; Steyaert, Swenson, et al., 2014; Wielgus & Bunnell, 1995). Alternatively, diurnal movement may provide easier accessibility to food sources which are occupied by other bears during the night. This assumption is in accordance with findings by Klinka and Reimchen (2002) and Kaczensky et al. (2006), who suggest that diurnal activity of females with offspring can be advantageous in relation to food accessibility and offspring safety. We found a significant increase in movement rates of females with dependent offspring for all periods of the day during hyperphagia, which is possibly related to increased mobility and nutritional needs of offspring.

Our results suggest that movement patterns of adult bears (males and solitary females) during the mating season are strongly influenced by mating behavior, whereas subadults males and females with dependent offspring modify their movement in order to disperse or to reduce infanticide risk. During the hyperphagia season, these behavioral differences in movement distances and probability of movement between reproductive classes disappeared (support prediction iv), and movement seemed mostly driven by food search. In addition, bear movement patterns may be affected by feeding stations and tourism. Additional research is needed to better understand bear movement ecology in areas with supplemental feeding programs and rapidly increasing tourism.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Neda Bogdanović: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Validation (equal); Writing-original draft (lead); Writing-review & editing (equal). **Anne G Hertel:** Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Supervision (equal); Validation (equal); Writing-original draft (supporting); Writing-review & editing (equal). **Andreas Zedrosser:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Supervision (equal); Validation (equal); Writing-original draft (supporting); Writing-review & editing (equal). **Milan Paunović:** Investigation (equal); Writing-review & editing (equal). **Milan Plećaš:** Data curation (equal); Investigation (equal); Writing-review & editing (equal). **Duško Ćirović:** Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Supervision (lead); Validation (equal); Writing-original draft (supporting); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

All the data used in the analyses are deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.cz8w9gj4j).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

2. Cozy den or winter walk: the effects of climate change and supplementary feeding on brown bear winter behavior

Paper II

ORIGINAL RESEARCH

Cozy den or winter walk: the effects of climate and supplementary feeding on brown bear winter behavior

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Abstract

Hibernation is a key adaptation for coping with unfavorable climatic conditions and low food availability in areas with severe winter conditions. While understanding the physiology and phenology of this adaptation has received considerable attention, comparatively little information is available on how hibernation will be affected by changing climate conditions. We used GPS telemetry data from 20 free-ranging brown bears monitored over 31 winters between 2007 and 2022, to identify behavioral strategies of bears during winter. We applied behavioral change point analysis to quantify brown bears' hibernation phenology in a population close to the bear's southern latitudinal range limit in Europe where supplementary food is available to bears year-round. We observed winter behavior patterns that varied across age and reproductive classes but also within individuals between winters. Among 31 winter events, we registered six cases in which bears exhibited a single hibernation/stationary period and 19 events where hibernation was split into up to five stationary periods. Moreover, six winter events did not show behaviors consistent with hibernation and individuals remained partly or completely active throughout winter. The movement of these active bears decreased with increasing snow depth. In addition, these winter-active bears showed higher fidelity to supplementary feeding sites during the winter period compared to the rest of the year. Our data suggest that an abundance of human-provided food resources during winter may facilitate the emergence of different wintering strategies in brown bears. Furthermore, supplemental feeding sites in combination with predicted mild winters and prolonged natural food availability suggest that the use of hibernation as an energy-saving strategy to overcome severe environmental conditions may decrease in the future.

Introduction

Animals have developed several strategies to cope with severe environmental conditions, such as drought or winter. For example, migration, that is, the seasonal movement from one habitat or area to another in search of food or more favorable conditions (Avgar et al., 2014; Mysterud et al., 2011; Pulido, 2007), or resistance, which entails remaining at the location and holding out the severe conditions through various adaptations (Blix, 2016). A third strategy is to reduce body temperature and metabolic rate and overcome periods of limited energy availability in a state of heterothermy (i.e., torpor; Geiser, 2004). Although heterothermy is generally assumed to occur either daily (less than 24 h; *daily heterotherm*) or seasonally as consecutive multi-day torpor (*hibernation*) (Geiser, 2013; Geiser & Ruf, 1995; Lyman, 2013; Nowack et al., 2017; Ruf & Geiser, 2015), there is a growing evidence for the existence of heterothermic continuum in mammals (Boratynski et al., 2019; Boyles et al., 2013; van Breukelen & Martin, 2015). Northern latitudes as well as mountainous areas are characterized by more severe environmental conditions, especially during winter periods, with long periods of snow cover and associated low ambient temperatures. In such environments, hibernation represents a trade-off to ensure the conservation of sufficient amounts of energy to survive severe conditions while minimizing the costs imposed by this

physiological state (e.g., reduced immune function, dehydration, freezing, higher susceptibility to predation, etc.) (Boyles et al., 2020; Humphries et al., 2003). Most hibernating mammals are comparatively small and have a large surface-to-volume ratio, making their thermoregulatory costs at low ambient temperatures prohibitively high (Geiser, 2013). Therefore, hibernating mammals usually go in a den/burrow during the unfavorable time periods and suppress their metabolic activity and energy expenditure to <15% (Geiser, 2004). Depending on how the hibernation state is induced, species can be classified into two categories: obligate hibernators (e.g., white-tailed prairie dog (*Cynomys leucurus*), European ground squirrel (*Spermophilus citellus*), Alpine marmot (*Marmota marmota*)), in which hibernation occurs predictably each year and is triggered by photoperiod and circannual rhythms (Harlow, 1995; Körtner & Geiser, 2000; Lehmer et al., 2001; Williams et al., 2014); and facultative hibernators (e.g., black-tailed prairie dog (*Cynomys ludovicianus*), Syrian hamster (*Mesocricetus auratus*), eastern chipmunk (*Tamius striatus*)), in which hibernation is elective and displayed only under certain environmental conditions (Chayama et al., 2016; Harlow, 1995; Harlow & Frank, 2001; Lehmer et al., 2006; Staples, 2014). Food and water availability (Harlow & Menkens Jr., 1986; Pigeon et al., 2016), ambient temperature and snowfall (Evans et al., 2016; Manchi & Swenson, 2005), as well as sex and reproductive status (Derocher et al., 1990; Haroldson et al., 2002), have been suggested as the most important factors affecting hibernation and determining its duration in facultative hibernators.

Ursids have a special position among hibernators, as they are comparatively large but also the only mammals that do not eat or drink, defecate or urinate, and even give birth during hibernation (Linnell et al., 2000). Bears are considered facultative hibernators, that is, they enter hibernation due to severe environmental (cold temperatures, snow) or physiological stressors (lack of adequate food resources) (Harlow, 1995). All energy required during hibernation is obtained from fat reserves, which results in a total 8–20% weight loss by den emergence. This loss can be twice as high (25–40%) in females that give birth and lactate in the den (Farley & Robbins, 1995; López-Alfaro et al., 2013), and may increase with age (Kingsley et al., 1983). Compared to small hibernators (such as ground squirrels, marmots, or hamsters) that may drop their body temperature to close to 0°C (Hellgren, 1998; Nelson & Robbins, 2015), bears experience just a comparatively small temperature decline (from ∼37°C to ∼33°C) during hibernation (Evans et al., 2016; Tøien et al., 2011). This allows bears to rapidly increase their heart rate and become mobile if needed during hibernation (Linnell et al., 2000), contrary to usually nonresponsive smaller hibernators (Nelson & Robbins, 2015).

Hibernation in brown bears is correlated with latitude, and bears at northern latitudes generally enter the den earlier and spend more time in hibernation (up to 7 months) compared to bears at southern latitudes (from 1.5 months to 4 months) (Graham & Stenhouse, 2014; Kaczensky et al., 2006; Manchi & Swenson, 2005; Nores et al., 2010). The mechanisms driving brown bear hibernation behavior are complex interactions between external (food availability and climate conditions) and internal factors (sex, reproductive status, age, physical condition) (Evans et al., 2016; González-Bernardo et al., 2020; Krofel et al., 2017; Manchi & Swenson, 2005). All age and sex classes in brown bears hibernate during at least parts of the winter (González-Bernardo et al., 2020), in comparison to the closely related polar bears (*Ursus maritimus*), where denning behavior is exclusively exhibited by pregnant females around their date of parturition (Atkinson & Ramsay, 1995; Ramsay & Stirling, 1988). However, in brown bears, some individuals (usually males) may remain occasionally or constantly active during winter, especially in areas with mild winter conditions, or in areas where reliable food sources exist throughout the year (Bojarska et al., 2019; Krofel et al., 2017; Nores et al., 2010; Van Daele et al., 1990). Previous studies have also shown that bears can interrupt hibernation in response to natural (e.g., flooding, food availability) or human-caused (e.g., forestry, hunting, research activities) disturbances (Evans et al., 2012; González-Bernardo et al., 2020; Huber & Roth, 1997; Krofel et al., 2017; Linnell et al., 2000; Sahlén et al., 2015; Van Daele et al., 1990).

Supplementary feeding is a commonly used practice in many European countries, primarily as a management tool for ungulates (Oro et al., 2013; Selva et al., 2014). However, this management practice also has effects on non-target species, such as bears (Selva et al., 2017). Several studies have raised concerns about the possible influence of supplementary feeding on the winter behavior of bears, suggesting that the occurrence of non-hibernating individuals may be caused by the availability of supplementary feeding sites (Bojarska et al., 2019; Krofel et al., 2017; Selva et al., 2017). Rapidly changing climatic conditions may have important implications for hibernation behavior, especially in species where hibernation occurs as a facultative response to external stressors. As mean winter temperatures increase globally (IPCC, 2013), the quantity and quality of natural foods available to hibernators during the winter months may increase. In combination with supplementary feeding sites, this may significantly affect hibernation behavior of bears and the occurrence of non-hibernating individuals may increase in the future. In turn, this may affect female fecundity, cub survival, and the prevalence of human–bear conflicts.

Here, we analyze winter behavioral patterns of a brown bear population close to the species' southern latitudinal range limit in Europe (Serbia). Our main goal is to improve the understanding of the winter ecology of a hibernating species, especially the occurrence and behavior of non-hibernating individuals in relation to supplementary feeding sites. In Serbia, bears face a continental climate with cool winters (around 0°C) and heavy snowfalls in the mountains (on average 90 snow days), but winter conditions have become milder in recent years (Republic Hydrometeorological Service of Serbia, 2021). Bears are also exposed to intensive supplementary feeding, as both target (for conservation and research activities) and non-target species (for ungulate management). We used fine-scale GPS-monitoring data to quantify winter behavioral patterns of brown bears. Second, we focused on bears that remained active, that is, exhibited movement behavior during winter, analyzed their movement patterns, as well as identified

possible drivers causing this behavior. Specifically, we tested whether snow depth would affect winter movements and whether active bears use known supplementary feeding sites during winter. We hypothesized (1) that milder winter conditions with less snow cover will cause bears to remain active and forego hibernation; and (2) that bears who remained active during winter will spend significantly more time at supplementary feeding sites during winter compared to the rest of the year when natural food is more abundant.

Materials and methods

Study area

The study area encompassed $\sim$25 500 km^2 in western and south-western Serbia (Stari Vlah-Raška Mountain Range) and is part of the Dinaric-Pindos brown bear population range (Fig. 1; see also Bogdanović et al., 2021). The area is mountainous with deep river valleys and elevations ranging from 750 to 1500 m above sea level (Pavlović et al., 2017). Around 60% of the area is covered by forests, and the dominant tree species are oak (*Quercus* sp.), beech (*Fagus sylvatica*), silver fir (*Abies alba*), and Norway spruce (*Picea abies*) (Lakušić et al., 2021). The rest of the area is mainly covered with pastures, meadows, and orchards. Mean monthly temperatures range from -1.2°C in January to 19°C in August (Republic Hydrometeorological Service of Serbia, 2021). Snow cover in the mountain areas usually occurs from the end of November until late March/early April, with frequent melting periods in between, depending on the year. The area is sparsely populated and most humans live in a few villages, but there is a dense network of cabins which are inhabited mainly during the tourist seasons (summer and winter). The latest estimate indicates that $\sim$100 bears occupy the study area and that bears are increasingly spreading toward the central part of the country (Ćirović & Paunović, 2018). In Serbia, supplementary feeding is commonly used as a management tool for game species, mostly ungulates, as well as to support brown bear population recovery and damage control. High-energy foods, especially corn (*Zea mays*) and livestock carcasses, are not only provided to wildlife at numerous registered but also unregistered feeding sites year-round (Fig. 1).

Data collection

We captured and monitored a total of 20 brown bears in the period 2007–2022. Bears were equipped with GPS collars (Vectronic-Aerospace, Berlin, Germany) programmed to record a position at 1 hour (h) for 18 individuals and 3 h intervals for 2 individuals. We controlled for repeated measures by including a random effect for each bear winter (a total of 31 bear winter events). While individuals are likely not behaviorally independent for consecutive years, they are exposed to different environmental conditions which affects their behavior. Controlling for "Bearwinter" instead of "BearID" therefore accounts for short-term (i.e., one winter) consistency in behavior and accounts for more variance than "BearID" alone. Bears were grouped according to their age and reproductive status into five categories: adult males ($N_{\text{bearwinter}} = 11$), subadult males ($N_{\text{bearwinter}} = 11$), solitary females (i.e., entered and left the den alone; $N_{\text{bearwinter}} = 4$), females with cubs of the year (i.e., entered den alone but left it with cubs; $N_{\text{bearwinter}} = 4$), and females with yearlings (entered and left the den with dependent offspring; $N_{\text{bearwinter}} = 1$).

Environmental covariates

We obtained daily temperature and snow depth estimates for the entire study period from the Republic Hydrometeorological Service of Serbia. Climatic variables were collected at one meteorological station (Zlatibor Mountain, 1028 m a.s.l) which is located in immediate vicinity of the area where active bears were observed during winter. In addition, we obtained coordinates for 25 registered supplementary feeding stations within the main brown bear hibernation area; however, the true number of feeding stations is higher due to several unregistered stations. Among the registered feeding stations, four are intended for brown bears, while the rest primarily targets ungulate (mainly wild boar *Sus scrofa*) but are commonly visited by bears (according to GPS-monitoring and camera-traping data). Feeding stations operate year-round, and corn is the most common food subsidy. Besides corn, at feeding stations intended for bears, livestock carcasses are also provided when available.

Statistical analysis

Quantification of bear behavior during winter

Our first aim was to identify whether a bear hibernated, changed its hibernation location (assumed to be a den), or stayed active during the winter months. We used behavioral change point analysis (BCPA) of winter GPS telemetry data (Gurarie et al., 2009) to identify periods when bears were stationary (i.e., not moving) and thus likely hibernating. For this we used movement data collected from October 1, until May 31, resampled to a 12 h fix interval (2 positions/day). The collars of some bears malfunctioned in the middle of winter; therefore, we only included bears which were monitored for at least 4 of the 8 months. We were specifically interested in the exact dates on which bears became stationary, that is, seized movement, and became active again, that is, resumed movement. We first created a movement trajectory and calculated for every 12 h step (**T**) the associated turning angle (ψ) and estimated speed (**V**). These two input parameters were then decomposed into orthogonal components of persistence velocity $\mathbf{V}_p(t)$, a measure of tendency for movement to persist in a given direction, and turning velocity $\mathbf{V}_t(t)$, a measure of tendency for movement to go in a perpendicular direction in a given time interval (Gurarie et al., 2009):

$$\mathbf{V}_P(t) = \mathbf{V} * \cos(\mathbf{\Psi})$$

$$\mathbf{V}_t(t) = \mathbf{V} * \sin(\mathbf{\Psi})$$

A BCPA searches for change points in $\mathbf{V}_p(t)$ and $\mathbf{V}_t(t)$ by sweeping a user-specified moving window with a given "window size" across the time series and calculates the mean ($\mathbf{\mu}$)
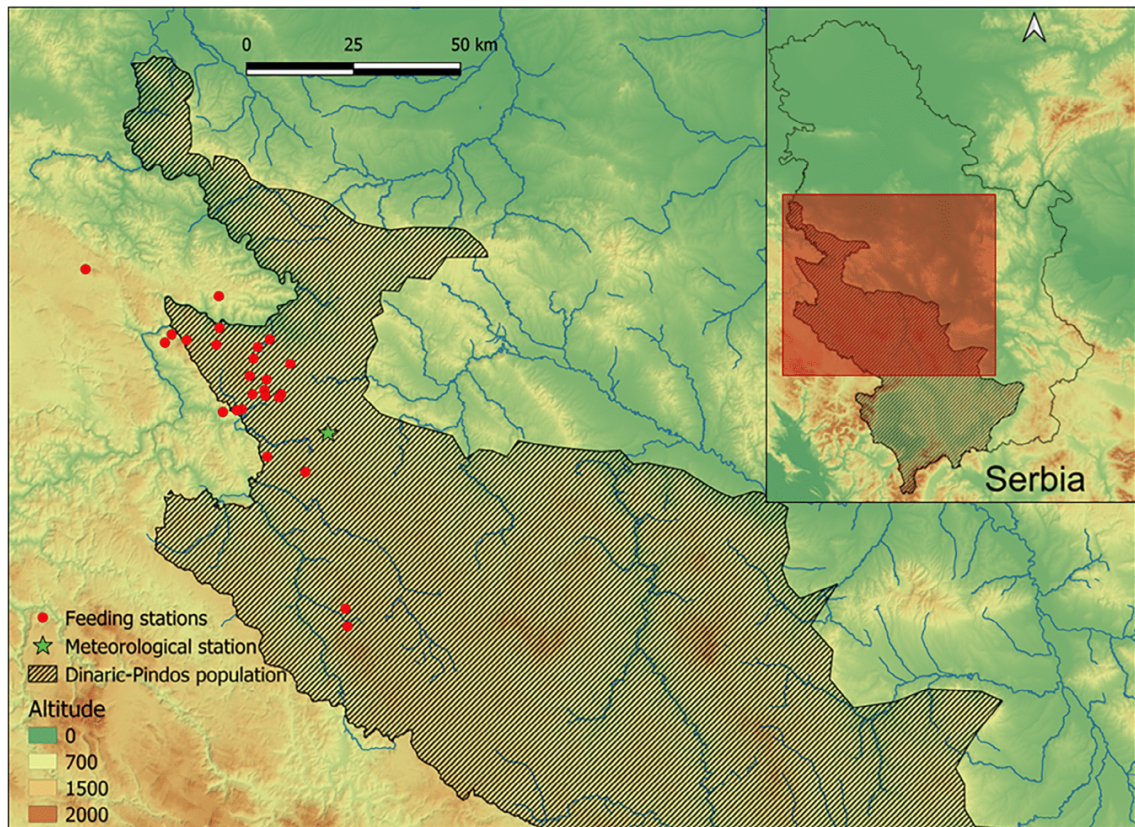
Figure 1 Study area (large map) with the current distribution range of the Dinaric-Pindos brown bear population (hatched area) in Serbia (small map), 2007–2022. Supplementary feeding sites are shown as red points, and meteorological station as green star.

and standard deviation (σ) of $V_p(t)$ and $V_t(t)$ for each animal location. For example, high values of $V_p(t)$ indicate fast and directed movement. There are several "tuning knobs" in BCPA, among which window size and sensitivity parameter (**K**) are the most important (Gurarie et al., 2009). Larger windows are generally more robust, while reducing the window size will provide more sensitive results. For the **K** parameter, the smaller this value the more likely it is that a simpler or null model will be selected (Gurarie et al., 2009). To identify stationary periods (likely suggesting hibernation behavior), we applied BCPA to each individual winter event. We set a moving window of six data points (3 days) and adjusted the **K** parameter to 3.

We assumed that a bear become stationary when both $\mu(V_p(t))$ and $\mu(V_t(t))$ approached 0 (i.e., when $\sigma(V_p(t))$ and $\sigma(V_t(t))$ was ±0.00015), while an increase of these parameters indicated a return to movement. If we failed to identify stationary periods, we increased **K** to 5 and repeated the analysis (Nicholson et al., 2019), and if we failed again to identify stationary periods, a bear was defined as active. We extracted the first and last date of stationary periods for all winter events and quantified their length. We defined bear as hibernating

when a stationary period was longer than 30 consecutive days, that is, the time required for body temperature to stabilize at ~33°C (Evans et al., 2016). Shorter stationary periods were defined as semi-active behavior. We verified all stationary locations (assumed to be dens) identified by the BCPA by visually inspecting the bears' GPS data. The algorithm missed two den switch events (i.e., a bear moved from one stationary location to another), likely due to the 12 h data resampling as well as missing GPS fixes. Therefore, we manually added these two events to our dataset. Finally, we summarized the first and last dates of all stationary periods as well as their total length for separate reproductive classes (i.e., adult and subadult males, solitary females, females with cubs of the year, and females with yearlings).

Winter behavior of active bears

In a second step, we focused on bears that remained active or exhibited semi-active behavior during the winter and applied a series of analyses to describe their behavior in relation to environmental covariates and food supplementation. We defined

active bears as those for which BCPA analysis failed to identify a stationary period and semi-active bears as those with cumulatively less than a month of stationary behavior.

We investigated if active and semi-active bears used supplementary feeding sites during the winter more often than during the rest of the year. For this, we quantified visits to feeding sites based on 3 h relocations for each month of the year. First, we created a 700 m buffer zone around each feeding site, which corresponds to the average 3 h displacement distance. We then calculated the proportion of a bear's monthly positions within these feeding site buffers (hereafter referred to as "monthly visitation rate"). We fitted a set of alternative linear mixed models (LMMs) with a Gaussian error distribution, a nonlinear polynomial term (1st, 2nd, and 3rd order) for month and accounting for bear ID with a random intercept, to evaluate whether the feeding site visitation rate varied during the course of a year. We selected the most parsimonious model based on the second-order bias-corrected Akaike's Information Criterion (AICc; Akaike, 1974), that is, models within a range of delta AIC 2 received most support (Arnold, 2010), where the model with the least number of parameters is considered as most parsimonious. We visually validated model assumptions that residuals were normally distributed.

We also aimed to assess the drivers of variation in daily movement distance. For each bear winter, we extracted daily estimates of snow depth (cm) and mean daily ambient temperature. We fitted a set of alternative LMMs explaining log-transformed daily movement distance with a nonlinear second-order polynomial term for Julian day and snow depth or mean ambient temperature. We also included a nonlinear relationship (second-order polynomial) for the distance to the nearest feeding station. Snow depth and temperature were negatively correlated (Spearman rank correlation = −0.6), and we therefore fitted models with either one of the two explanatory variables. All models were fitted with "Bearwinter" as random intercept to account for autocorrelation and individual variability. The most parsimonious model was selected based on AICc. All statistical analyses were conducted in the R software environment (version 4.1.2) using the packages bcpa (version 1.3.2; Gurarie, 2014), rgeos (version 0.5–9; Bivand, 2021), adehabitatLT (version 0.3.25; Calenge, 2006), and geosphere (version 1.5–18; Hijmans, 2019) (R Development Core Team, 2023).

Results

We analyzed winter behavioral patterns for 14 male and 6 female brown bears monitored over 1–3 years ($n = 31$ bear winter events). Overall, we detected large variability in winter behavior across the 31 bear winters (Fig. 2). We identified 25 winter events as hibernation (ranging from single hibernation event up to five events per winter), three winter events as semi-active with 30 or less days of inactivity (8, 18, and 30 days), and three winter events as constantly active (Fig. 2). In addition, we observed that some individuals monitored over a few years, displayed different behavioral patterns in consecutive winters.

For the 25 winter events with hibernation, the total time individuals spent hibernating ranged from 42 to 172 days (mean 97 days; Table 1), while the mean duration an individual spent at a given den location was 40 days (range: 1–163 days; Table 1). Hibernation chronology varied in relation to sex and reproductive status, with males displaying significantly shorter cumulative hibernating periods compared to females (mean ± SE; males: 80 ± 8 days, females: 128 ± 11 days). Adult and subadult males spent on average 80 ± 10 days (range: 42–138; $N = 7$; $N_{bearwinter} = 9$) and 79 ± 14 days (range 43–123; $N = 5$; $N_{bearwinter} = 7$) hibernating per winter, respectively. Among females, females with cubs of the year hibernated the longest (155 ± 8; range: 140–172; $N = 4$; $N_{bearwinter} = 4$), followed by the only monitored female with yearlings which spent a total of 136 days hibernating, while solitary females stayed in the den for 99 ± 13 days (range: 75–129; $N = 2$; $N_{bearwinter} = 4$; Fig. 3).

Den entry date varied over a 2-month period from November 5 to January 4 (median = November 23). Den exit ranged over a 4-month period from January 12 to May 24 (median = March 20, Fig. 2a). Males usually entered the den in the second half of November or December (median = November 28) and left the den in February or March (median = March 13), while females remained longer in the dens (November 19–April 17; Fig. 2a). Among females, solitary females entered the den later (median = December 2) and left it earlier (median = March 24), compared to females accompanied by dependent offspring of any age, among which females with cubs of the year were the last to leave the den (median = May 18; Fig. 2a).

Winter behavior of active bears

Out of 31 bear winters, we identified six instances of active behavior during the winter (Fig. 2b). In all cases, active winter behavior was displayed by males (3 adults, 3 subadults). Among them, three individuals did not show any sign of hibernating behavior; instead they stayed active during the entire winter period, while the other three bears showed semi-active behavior with short stationary periods (range: 1–26 days) during the winter months (Fig. 2b).

Use of supplementary feeding sites by brown bears during winter

The best performing model explaining the use of supplementary feeding sites over the year included a second-order polynomial for month (ΔAIC = 0.0, AICcw = 0.68; Table S1). In addition, the use of supplementary feeding sites among active and semi-active bears varied significantly between months ($\chi^2 = 38.46$, d.f. = 2, $P < 0.001$). Bears had a higher feeding site visitation rate during the winter compared to the summer months (Fig. 4). In January, active bears spend about 50% of their time close to the feeding sites, while time spent at feeding sites dropped to 10% in June and July (Fig. 4).

Movement of active bears during winter

Movement distance of active and semi-active bears was best described by a second-order polynomial for Julian day, snow
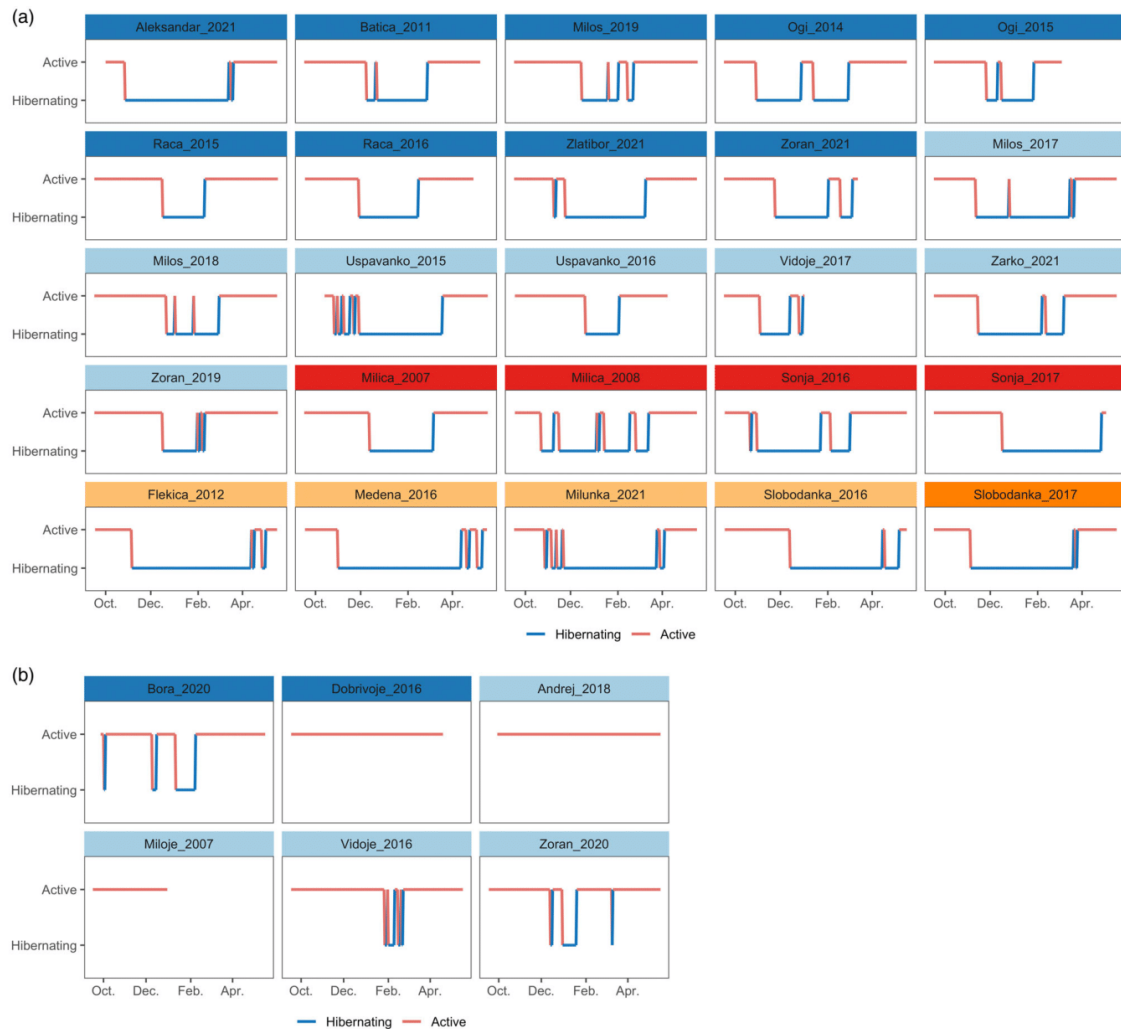
Figure 2 Brown bear hibernation chronology (a) and winter behavior patterns of active and semi-active bears (b) from Serbia, 2007–2022. Red lines represent active behavior and blue lines hibernating behavior. Different facet colors denote different reproductive classes (dark blue: adult males, light blue: subadult males, red: solitary females, light orange: females with cubs of the year, dark orange: female with yearlings).

depth, and distance to the nearest feeding station (ΔAIC = 0.0, AICcw = 1; Table S2). Both active and semi-active bears reduced their movement in the middle of the winter (Fig. 5a). Average daily movement distances were ∼3.6 km in October and dropped to ∼2.3 km in January (Fig. 5a). We also found that bears decreased their movement as snow depth increased and moved on average 1.1 km per day in 50-cm-deep snow, compared to no snow (daily average distance of 2.5 km; Fig. 5b). Last, we found that bears moved over shorter daily distances when close to a feeding station (on average 1.7 km per day) than when farther away (3.1 km at 10 km distance; Fig. 5c).

Discussion

Among 31 winter events of GPS-collared brown bears, we registered 6 cases in which bears exhibited a single hibernation/stationary period, and 19 events where hibernation was split into up to five stationary periods. Moreover, six winter events (by six males) did not show behaviors consistent with hibernation and remained partly or completely active throughout winter. The movement of these active bears, however, decreased with increasing snow depth. In addition, these bears showed higher fidelity to supplementary feeding sites during the winter compared to the rest of the year.

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**Table 1** Summary of winter activity patterns of GPS-collared brown bears in Serbia, 2007–2022

	N_{bears}	$N_{bearwinters}$
Bear reproductive status[a]		
Males	14	22
Adult males	9	11
Subadult males	7	11
Females	6	9
Solitary	2	4
With cubs of the year	4	4
With yearlings	1	1
Monitoring duration		
1 year	11	11
2 years	7	14
3 years	2	6
Winter behavior		
Active	3	3
Semi-active	3	3
Hibernating	16	25

	Total	At given den location
	N_{days}	N_{days}
General hibernation statistics		
Hibernation length		
Mean	97	40
Median	91	18
Range	42–172	1–163

[a]One bear can be included in several categories as it is monitored over several years.

Time spent in hibernation varied between 42 and 172 days in our study area, with males spending on average 37% less time in the den compared to females. This sex difference is a general pattern observed in several brown bear populations at different latitudes (Friebe et al., 2001; González-Bernardo et al., 2020; Krofel et al., 2017; Manchi & Swenson, 2005; Van Daele et al., 1990). Sex differences in hibernation onset, duration, and emergence have also been observed in several other hibernating species; however, unlike in bears, males are generally the first to enter hibernation (Healy et al., 2012; Kart Gür & Gür, 2015; Michener, 1992; Siutz et al., 2016). In bears, pregnant females are the first to enter the den, followed by non-pregnant females, and males are usually the last to enter hibernation (Friebe et al., 2001; Manchi & Swenson, 2005). The ultimate reason for earlier den entry of females and for differences in hibernation length between the sexes is that female bears gestate, give birth, as well as nurse the young up to several months during hibernation (López-Alfaro et al., 2013; Steyaert et al., 2012). In comparison, reproduction and parturition in most other hibernators usually occur after emergence from hibernation (Kusch et al., 2021).

We documented only male bears to remain active during winter in our study area, that is, all females hibernated, independent of reproductive status. Most bears reported in the literature that exhibit hibernation variations not caused by human disturbance, such as very short hibernation periods, den abandonment, or remaining active during winter, were males (Friebe et al., 2001; Graber, 1990; Krofel et al., 2017; Ramsay & Stirling, 1988; Van Daele et al., 1990). Male bears are
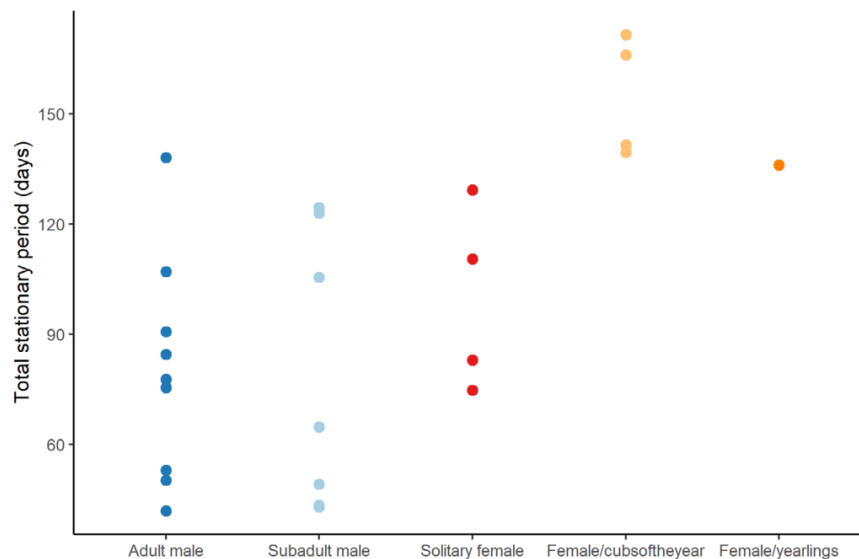
Figure 3 Total time (in days) spent stationary for different reproductive classes of GPS-collared brown bears with stationary behavior in Serbia, 2007–2022.
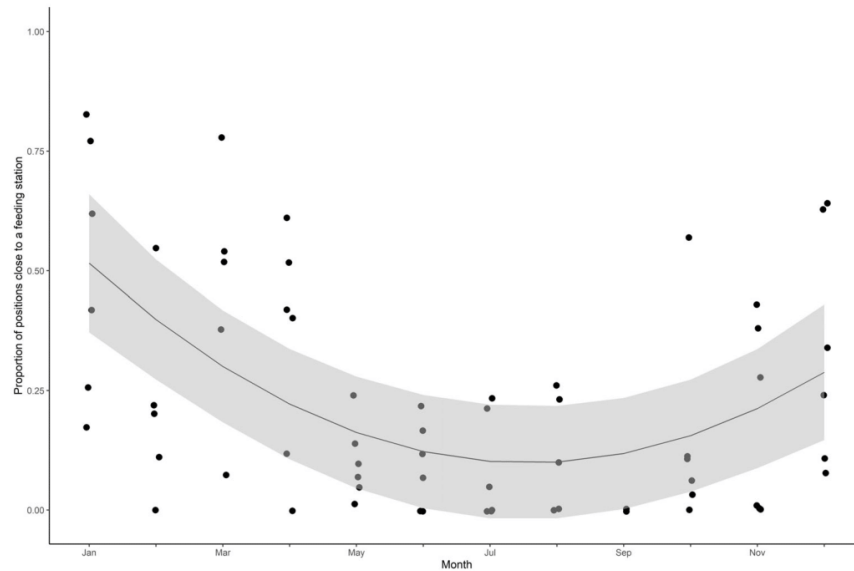
Figure 4 Predicted feeding site visitation rates across the year for active and semi-active GPS-collared brown bears (*n* = 6) in Serbia.
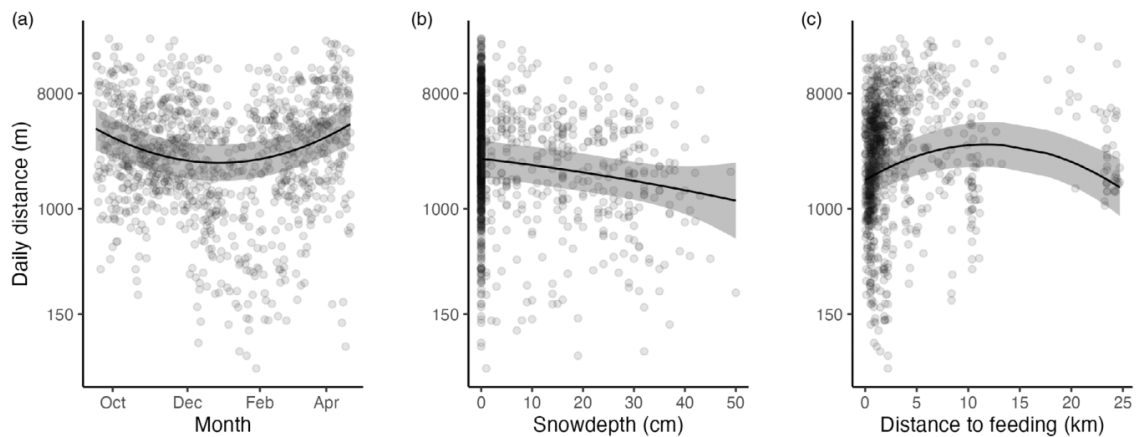

Figure 5 Predicted daily distances in relation to month (a), snow depth (b), and distance to the feeding station (c) for three active and three semi-active GPS-collared brown bears in Serbia (a total of 1085 daily distances used).

generally larger and have a higher absolute body fat content which helps them to endure harsher environmental conditions compared to females (Bojarska et al., 2019; Huber & Roth, 1997; Nores et al., 2010; Selva et al., 2017; Van Daele et al., 1990). Remaining active during winter has been observed in some other hibernating species, especially in southern parts of their distributional range (Harlow, 1997; Parkes, 1975). For example, black-tailed prairie dogs are regularly observed foraging above ground throughout the winter if

not exposed to low ambient temperature and severe food and water deprivation (Harlow, 1997; Harlow & Menkens Jr., 1986). Our results showed that daily movement distances decreased by 30% in all winter-active individuals from October to January and with increasing snow depth. A decrease in movement rates due to harsher weather conditions (i.e., low ambient temperature, snow cover) is a common response of many winter-active species as it conserves energy (Beier & McCullough, 1990; Trondrud et al., 2021; Van Beest

et al., 2013; Webb et al., 2010). Yet, these results should be interpreted carefully as climate data were collected at only one meteorological station and may not accurately capture variation in climatic conditions across our study area. However, used weather station is the only station that was located within reasonable distance from our study area and thus reflects the local conditions most appropriately.

Contrary to previous studies (Bojarska et al., 2019; Evans et al., 2016; González-Bernardo et al., 2020), our results show that some individual bears stayed active despite low ambient temperature and snow, which has also been recorded for brown bears in the Cantabrian Mountains, Spain (Nores et al., 2010). It remains unclear why some bears chose to stay active throughout winter in some years while others have not. Our results show further that the same individuals may choose different wintering strategies in other years, which might support the hypothesis about a heterothermy continuum (Boratynski et al., 2019; Boyles et al., 2013; van Breukelen & Martin, 2015). However, these results have to be interpreted carefully due to the restricted sample size which emphasizes the importance of further research on bear hibernation phenology. The fact that individuals exposed to the same environmental and food conditions use different behavioral and physiological strategies within and among winters challenges the general notion that environmental conditions in combination with the availability of food resources regulate the initiation of den entry in bears (Linnell et al., 2000; Manchi & Swenson, 2005). Furthermore, Boyles et al. (2020) hypothesized that if an animal is able to fulfill its energy requirements during winter (due to abundant food resources), then initiating hibernation would be too energy consuming, and remaining euthermic would be energetically more beneficial. Also in other facultative hibernators, such as black-tailed prairie dogs, it has been shown that cold temperature is not enough to induce hibernation unless combined with food and water deprivation (Harlow & Menkens Jr., 1986).

In addition to climatic conditions, a primary driver of winter activity observed in our study area likely is the availability of high-quality food at supplementary feeding sites. All winter-active bears regularly visited feeding sites, and the use of these sites was more pronounced during winter compared to other seasons. Prolonged food availability has been linked to a delay in the onset of hibernation, reduction of hibernation length, or its frequent disruption in other bear populations (Krofel et al., 2017; Nores et al., 2010; Selva et al., 2017; ŠtofÍk et al., 2016; Van Daele et al., 1990). For example, Krofel et al. (2017) found that the hibernation length of brown bears with access to feeding sites in Slovenia decreased 45–56% compared to the expected hibernation duration for that latitude ($\sim$130 days for males and $\sim$150 days for females). This observed reduction in hibernation likely is related to the high availability of food at diversionary feeding sites in Slovenia, and individuals that disrupted hibernation showed an increased use of feeding sites (Krofel et al., 2017). Hibernation disruptions have also been observed in other European countries where bears have access to supplemental feeding sites during autumn and winter (Bojarska et al., 2019; Kavčič et al., 2015; Selva et al., 2017; ŠtofÍk et al., 2016).

Furthermore, several studies have shown that abundant natural food sources during the hibernation period might also cause bears to shorten or forgo hibernation (Nores et al., 2010; Van Daele et al., 1990). In particular, male brown bears on the Kodiak Archipelago, USA, are regularly observed outside the den in the first part of the winter during mild winters with extended periods of natural food availability (Van Daele et al., 1990). Consequently, it can be expected that alterations in hibernation duration in the future will not be restricted to areas with supplementary feeding but might become a ubiquitous phenomenon.

Our data further show that some individuals interrupt hibernation one or several times throughout the winter. The ultimate causes for interruptions of the hibernation period remain unclear, but bears have been documented to abandon their dens due to natural or anthropogenic disturbances or when exposed to abundant food sources (Friebe et al., 2014; Huber & Roth, 1997; Krofel et al., 2017; Linnell et al., 2000; Nores et al., 2010; Swenson et al., 1997; Van Daele et al., 1990). Food-related hibernation alterations have also been observed in other facultative hibernators, for example, eastern chipmunks reduced both the depth and duration of hibernation if sufficient energy reserves have been accumulated (Munro et al., 2008). We cannot rule out human disturbances, however, given the remoteness of most den sites and the existence of supplementary feeding sites in the study area, the availability of food resources seems the more likely explanation. Independent of the causes, prolonged winter activity of bears may lead to an increase in human–wildlife conflicts (Johnson et al., 2018; Krofel et al., 2017, 2020; Pigeon et al., 2016). In our study area, permanent food supplies at spatially predictable locations seem to govern bear movement decisions during winter as bears repeatedly visited different feeding sites throughout the winter. While we do not know how frequently food is provisioned at each site, the observed movement patterns imply that enough food is available or that food provisioning is continuous throughout winter. In addition, the recursive visitation behavior suggests that memory plays an important role in the movement decisions of bears (Fagan et al., 2013). These authors showed that memorizing specific food-rich locations improves weight gain per time unit as it reduces search time (Fagan et al., 2013).

Conclusions

Our data suggest that an abundance of human-provided food resources during winter may facilitate the emergence of four wintering strategies in brown bears: an obligate hibernation strategy with individuals hibernating for the entire winter for females that give birth or are accompanied by dependent offspring; a facultative hibernation strategy where individuals of non-reproductive sex and age classes chose to hibernate all winter; a facultative intermittent strategy with periods of hibernation interrupted by short periods of activity; and an active strategy where individuals remain active for the entire winter. Globally changing climate conditions will cause milder winters in the future which will inevitably lead to a prolonged availability of natural food resources, in addition to supplemental

feeding sites (IPCC, 2013; Williams et al., 2008). This suggests that the use of hibernation as an energy-saving strategy under such conditions might become energetically more demanding compared to remaining euthermic (Boyles et al., 2020). Given that bears are the only species that give birth during hibernation, the question arises whether these human-induced changes may affect female reproductive success, and ultimately population viability. Furthermore, prolonged bear activity may increase frequency of human–bear interactions and damages. We hope that our results will initiate a much-needed debate about how the effects of climate changes in combination with the widespread practice of wildlife supplemental feeding may affect the winter behavior and ultimately the life history of bears and other hibernating species.

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Conflict of interests

The authors declare no competing interests.

Author contributions

NB and DĆ collected the data and initiated the study. NB and AGH designed methodology. Data analysis and preparation of figures was done primarily by AGH and NB. NB led the writing of the manuscript, and AZ, AGH, and DĆ revised the manuscript extensively. All authors contributed substantially to the study and gave final approval for publication.

Data availability statement

The data used and analyzed in this study are available from D. Ćirović on reasonable request due to conservation reasons and

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Model selection results evaluating whether feeding sites visitation rate differed over the year for active and semi-active brown bears in Serbia. Evaluating metrics include AICc (Akaikes Information Criterion corrected for small sample sizes), ΔAIC (difference in AICc between the best model (smallest AICc) and each model) and AICc weight (relative likelihood of a model).

Table S2. Model selection results evaluating effects of environmental covariates (snow depth and ambient temperature) and distance to feeding station on bear movement during winter period. Evaluating metrics include AICc (Akaikes Information Criterion corrected for small sample sizes), ΔAIC (difference in AICc between the best model (smallest AICc) and each model) and AICc weight (relative likelihood of a model).

3. Where to go? Habitat preferences and connectivity at a crossroad of European brown bear metapopulations

Paper III

Where to go? Habitat preferences and connectivity at a crossroad of European brown bear metapopulations

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ABSTRACT

Natural habitats become increasingly degraded and fragmented due to rapid human expansion. The decreasing availability of high-quality habitats combined with a lack of connectivity among suitable patches and the low permeability of human-transformed landscapes endangers the survival of many species. Understanding the environmental conditions favoring a species' distribution and the identification of movement corridors between populations is crucial for sustainable conservation and management. Serbia is the only European country inhabited by three different brown bear metapopulations, highlighting its crucial geographical position for establishing functional connections among these metapopulations. We used species distribution modeling to predict suitable habitats for the three bear metapopulations in Serbia at two spatial scales (5 and 1 km²). We combined the predictions from each metapopulation to define suitable habitats for range expansion. Further, we created landscape resistance maps to identify possible connectivity areas to promote gene flow between these metapopulations. Our results highlight that 1) the underlying processes of bear habitat selection at the coarse scale differ between metapopulations, mainly due to the differences in habitat availability; 2) > 60% of areas predicted as suitable for bears in Serbia are currently still unoccupied; 3) the south-eastern part of Serbia represents a key area for the connectivity between bear metapopulations in the future. However, the presence of several movement barriers, such as highways, highlights the need to implement adequate mitigation measures to increase habitat permeability. Because bears are a useful umbrella species for conservation actions, improvement of habitat quality and permeability will also positively affect many other species in this region.

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1. Introduction

Expansion of human activities into wildlife habitats together with rapid development of infrastructure has led to the transformation of natural habitats into a network of fragmented and isolated patches (Bennett, 2003). Habitat connectivity is among the most

Fig. 1. Distribution range of brown bear metapopulations (Carpathian, Dinaric-Pindos, East-Balkan) in Serbia and southeastern Europe (Source: https://www.iucnredlist.org/species/41688/121229971).

important factors affecting the viability of wildlife populations, especially in recent years, when human-derived habitat degradation and fragmentation has reached critical levels that threaten the survival of many species (Fisher and Lindenmayer, 2007; Cushman et al., 2013; Saura et al., 2014; Mateo-Sánchez et al., 2014). As a result, many species with large area requirements exist in
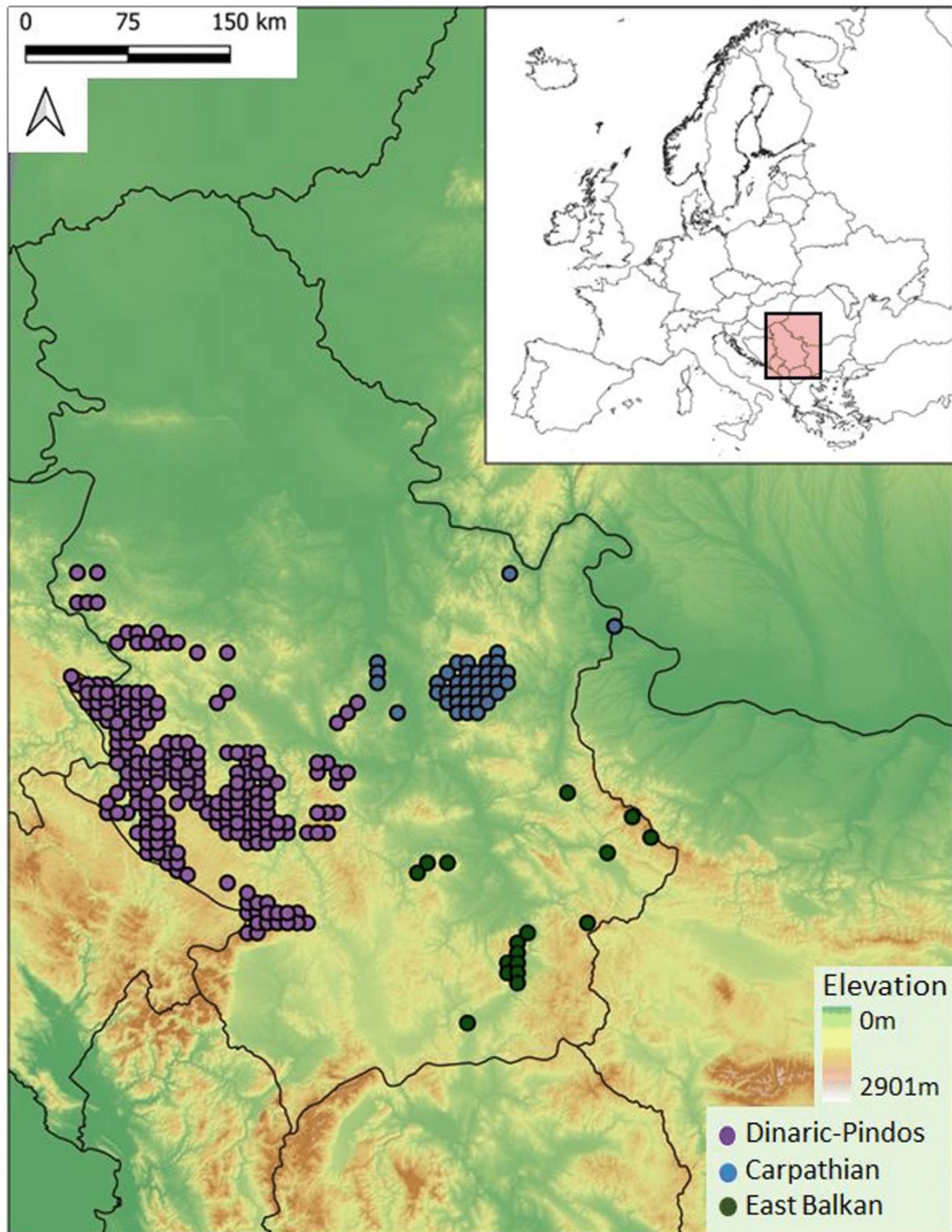

Fig. 2. Distribution of brown bear occurrence data at the regional 5 × 5 scale collected in Serbia, 2007–2021. The color-coding of the data points refers to data collected in different brown bear metapopulations (Dinaric-Pindos, Carpathian, East Balkan) in Serbia.

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metapopulations, making them vulnerable to reduction in gene flow, demographic stochasticity, and extinction (Lande, 1988; Hanski, 1998; Melbourne and Hastings, 2008). The long-term viability of such metapopulations largely depends on establishing functional connectivity across fragmented landscapes (Lancaster et al., 2016; Cushman et al., 2018). Conservation strategies commonly rely on the designation of protected areas, which, even if essential, may not be enough to preserve metapopulations (Coetzee, 2017). Furthermore, as many wide-ranging species occur across areas with different political jurisdictions and population management regimes, conservation strategies must be carried out at the appropriate scale to ensure long-term population viability (Inman et al., 2013). Thus, determining a species' current and potential distribution as well as identifying suitable habitats and movement corridors is crucial for sustainable management and conservation (Akçakaya et al., 2007; Martin et al., 2012; Zarzo-Arias et al., 2018; Kouchali et al., 2019).

Large carnivores, such as the brown bear (*Ursus arctos*), grey wolf (*Canis lupus*), and Eurasian lynx (*Lynx lynx*), used to have a pan-European distribution but were hunted to extinction or strongly reduced up until the beginning of the 20th century (Boitani and Linnell, 2015). Due to changes in conservation attitudes especially in the second half of the 20th century, populations of these species are currently recovering and recolonizing former distribution areas across Europe (Chapron et al., 2014; Ordiz et al., 2021). Due to the lack of suitable and reasonably large protected areas, the conservation of large carnivores must mainly occur outside of protected areas in coexistence with humans (Chapron et al., 2014). Large carnivores are wide-ranging species that require large areas but are able to coexist with humans in areas with moderate human densities and activities (Chapron et al., 2014). However, due to the high fragmentation of European landscapes, maintenance of connectivity and gene flow between populations is of crucial importance for the conservation of viable large carnivore populations (Crooks and Sanjayan, 2006; Dixon et al., 2007; Mateo-Sánchez et al., 2014; Fletcher et al., 2018).

Brown bears exist in 10 metapopulations across human-modified landscapes in Europe (Swenson et al., 2000; Zedrosser et al., 2001; Penteriani et al., 2018). Bears have very large spatial requirements, i.e., male home ranges can be up to several thousand square kilometers (Dahle and Swenson, 2003; Ćirović et al., 2015), and are highly affected by habitat loss and fragmentation (Nellemann et al., 2007; Calvignac et al., 2009; de de de Gabriel Hernando et al., 2021). Therefore, improving habitat permeability and establishing connectivity between suitable habitat patches and populations is a priority for brown bear conservation in Europe. Serbia is located in south-eastern Europe and is of special strategic importance for bear conservation, as it is the only country where three of the largest European metapopulations, i.e., Carpathian, Dinaric-Pindos, and East-Balkan, have a potential contact zone (Kaczensky et al., 2013; Chapron et al., 2014; see also Fig. 1). Therefore, the identification of suitable areas and habitats in Serbia where these metapopulations could expand to and potentially inter-connect, presents a unique opportunity for brown bear conservation in Europe.

We used habitat suitability models with a maximum entropy approach (MaxEnt) to analyze bear habitat selection patterns at a coarse regional (5 ×5 km) and a fine local scale (1 ×1 km) in an area where three European brown bear metapopulations (from now on referred to as populations) meet in Serbia. We aimed to 1) determine which environmental variables drive bear habitat selection in each population, due to different habitat availabilities; 2) create a combined prediction to define suitable bear habitats and possible expansion areas in Serbia; 3) explore areas of possible population connectivity based on landscape resistance; and 4) compare the results with the current distribution of bear populations and the existing network of protected areas in Serbia to evaluate if these areas could function as stepping stones to guide in population connectivity.

2. Material and methods

2.1. Study area and bear metapopulations

The study was conducted in Serbia, which is located in southeastern Europe (Fig. 1) and covers 88,361 km^2. The country is characterized by lowlands (from 28 to 200 m above sea level; 36.7% of the territory) in the north and mountainous areas in the rest of the country, including the Dinaric Mountain Range, the Serbian part of the Carpathian Mountain Range, the Balkan Mountain Range, and the mountains of the Vardar region (Pavlović et al., 2018). Forests occupy 25.6% of the territory, mainly composed of deciduous and mixed beech-coniferous forests, and to a lesser extent coniferous forests. The rest of the territory is occupied by developed agricultural lands (39.7%) and other lands, including undeveloped agricultural and barren lands or infrastructure areas, among others (34.7%; Statistical Yearbook of the Republic of Serbia 2021). Topographic differences can be observed among the mountainous part of the country, where the south and west are characterized by higher and steeper terrain (up to 2656 m at Mt. Djeravica), compared to the east (up to 1339 m at Mt. Beljanica). Serbia has a continental climate with temperatures ranging from − 20 °C in winter up to 40 °C during summer and a mean annual precipitation of 724 mm (Smailagić et al., 2013; Pavlović et al., 2018).

Serbia is the only European country inhabited by three different brown bear populations (Fig. 2), which indicates its crucial geographical importance for establishing connectivity and enhance the long-term conservation of the species in Europe. Brown bears are strictly protected in Serbia. Bears in the western and south-western part of the country are part of the large Dinaric-Pindos population, with an estimated size of > 3000 individuals distributed from Slovenia in the north to Greece in the south (Kaczensky et al., 2013; Chapron et al., 2014). The current population size estimate in the Serbian segment of the Dinaric-Pindos population is 60 ± 10 individuals (Kaczensky et al., 2013). The eastern part of the country is inhabited by bears belonging to the Carpathian population, which Serbia shares with Romania, Ukraine, Poland, and Slovakia. This is the largest European bear population with an estimated population size of > 7000 individuals (Kaczensky et al., 2013; Chapron et al., 2014). The current population size estimate for this population in Serbia is 6 individuals (Kaczensky et al., 2013). Individuals in the south-east of Serbia are part of the East-Balkan population with ∼ 600 individuals distributed in Bulgaria, North Macedonia, Greece, and Serbia. This is the smallest population segment in Serbia and it is estimated at 2–3 individuals (Kaczensky et al., 2013). Latest data from the Serbian National Bear

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Management Plan indicate an increase in both the number of individuals and range of all three populations in Serbia (Ćirović and Paunović, 2018), however, no connectivity or gene flow between the populations has been documented (Bogdanović et al. 2021).

2.2. Statistical analysis

Species distribution modeling (SDM) is commonly used to associate a species' known distribution data with environmental variables that describe it's occurrence (Anderson et al., 2003; Elith and Leathwick, 2009; Cassini, 2011). These models provide the opportunity to study habitat suitability of a species' potential range and to focus conservation efforts in areas that are most cost-effective for the long-term survival of the species (Martin et al., 2010; Mateo-Sánchez et al., 2014). We used two types of bear presence data: 1) GPS telemetry data, and 2) occurrence locations collected directly by remote cameras or indirectly (i.e., feces, footprints, hair). Remote cameras were located in all areas with bears in Serbia and an occurrence location was defined as the photograph of a bear for at least one time. Telemetry data included GPS locations (1 h relocation interval) of 20 brown bears from the Dinaric-Pindos and Carpathian populations monitored during 2007–2021 (Bogdanović et al. 2021). The permit for capture and handling was provided by the Serbian Ministry of Environmental Protection (license number: 353–01–127 1053/2019–04). To evaluate potentially suitable habitats for bears, we used coarse (5 ×5 km) and fine (1×1 km) grid cell sizes, because bears might be affected by environmental characteristics at different spatial scales (Mateo-Sánchez et al., 2013; Zarzo-Arias et al., 2019). At both the coarse and fine spatial scale, we selected the center coordinates of the grid cells with at least one bear occurrence. These coordinates were used as "bear presence" input data in our models.

2.3. Environmental variables

We used 12 environmental variables related to topography, land cover and human infrastructure (Table 1).

Elevation data (DEM) were obtained from DIVA GIS website (https://www.diva-gis.org/gdata), and mean aspect of slopes was estimated using Geographic Information System software (QGIS, version 3.16.15; QGIS Development Team, 2020). Transportation network data (highways, local roads, forest roads, hiking trails) and water bodies (rivers and streams) were obtained from the Geofabrik website (https://download.geofabrik.de/europe/serbia.html). Variables containing distances to habitat features were calculated as the Euclidean distance from each cell centroid to the nearest habitat feature in question. We calculated variables containing percentages of vegetation land cover classes based on the CORINE Land Cover Map of Europe (1:100.000) (available at: https://land.copernicus.eu/pan-european/corine-land-cover). Protected areas cover 6914 km^2 (7,81%) of Serbia ranging from 1133 km^2 (Stara Planina Mountain) to 9 km^2 (Mali Vršački Rit) (information provided by the Institute for Nature Conservation of Serbia, https://www.zzps.rs/).

We checked for spatial correlation and variance inflation factor (VIF) between variables to avoid inaccurate model predictions (Snee, 1977; Peterson et al., 2007). In case of high Pearson correlation coefficients (> 0.7) and high VIF's (>5) we retained the variable that was more important for bear biology according to the scientific literature (Trisurat et al., 2012; Zarzo-Arias et al., 2019). For the final modeling procedure, we used a total of 10 uncorrelated variables: elevation, distance to water bodies, distance to first-order (highways), second-order (regional and local roads) and third-order (forest roads and hiking trails) roads, distance to urban areas, % forest, % shrubland, % pasture, and % human infrastructure (e.g., industrial areas, green urban areas, sport facilities).

2.4. Modeling habitat suitability

To predict suitable bear habitats, we used the maximum entropy modeling approach (MaxEnt version 3.4.1; Philips et al., 2007) called from the statistical environment R (version 4.0.4; R Core Team, 2021) using the packages dismo (version 1.3.5; Hijmans et al., 2021) and ENMeval (version 0.3.1; Muscarella et al., 2014). This method is commonly used for modeling species distribution and predicting potentially suitable habitats (Zarzo-Arias et al., 2019; Evcin et al., 2019; Rozhnov et al., 2020). To obtain the best model structure, we created candidate models for each bear population with all feature type combinations (i.e., linear, quadratic, product,

Table 1
Description, source, and original format of 12 environmental variables used to evaluate habitat suitability in three brown bear metapopulations in Serbia. Variables marked with * are correlated and removed from further modelling.

Layer name	Layer description	Source	Format
Altitude		DIVA-GIS	Raster
Slope*		ArcGIS	Vector
Roads 1	Distance to nearest highways	GEOFABRIK	Vector
Roads 2	Distance to nearest local roads	GEOFABRIK	Vector
Roads 3	Distance to nearest forest roads and trails	GEOFABRIK	Vector
Water	Distance to nearest water bodies	GEOFABRIK	Vector
Urban	Distance to nearest infrastructure	CORINE Land Cover	Vector
Forest	% of forests per grid cell	CORINE Land Cover	Vector
Pasture	% of pastures per grid cell	CORINE Land Cover	Vector
Scrub	% of scrubs per grid cell	CORINE Land Cover	Vector
Infrastructure	% of infrastructure per grid cell	CORINE Land Cover	Vector
Agroland*	% of agriculture per grid cell	CORINE Land Cover	Vector

threshold, hinge (Phillips et al., 2006, Philips et al., 2007)), each one run over a set of regularization multipliers ranging from 0 to 19. We applied the same set of 10 environmental variables in all models. We used 500 iterations, a convergence threshold of 10^{-5}, values from all grid cells for the entire area as background, and the c-loglog format as model output, which allows us to interpret predictions as probability of bear occurrence ranging from 0 (unsuitable habitats) to 1 (highly suitable habitats) (Phillips, Dudík, 2008). We used Akaike's Information Criterion corrected for small sample sizes (AICc) to select the most parsimonious model for each population (Akaike, 1974; Burnham and Anderson, 2002). All models within 2 Δ AICc units were considered as equally good, and we considered the model with the least number of parameters as the most parsimonious (Burnham and Anderson, 2002; Zarzo-Arias et al., 2019). We obtained the percentage contribution of each variable to the model based on a heuristic method provided by default by MaxEnt (Phillips et al., 2006). Finally, we created one final model by combining the predictions from all bear populations (hereafter combined model). For that purpose, we retained only the highest predicted habitat suitability values from each population at both scales (Zarzo-Arias et al., 2022). Further, we defined a suitable/not-suitable threshold as the mean predicted suitability value for grid cells with confirmed bear presence.

2.5. Model validation

We used the area under the curve (AUC) of the receiver operating characteristics (ROC) curve for evaluating model performance (Fielding and Bell, 1997; Phillips et al., 2006). AUC values range from 0 to 1, where values close to 0.5 indicate that the model performance is not better than the random model (Phillips et al., 2006), while values from 0.7 to 0.9 indicate models with moderate performance, and values above 0.9 denote excellent predictive ability (Pearce and Ferrier, 2000). We followed Muscarella et al. (2014) for model execution and used a 'Checkerboard1′ method to separate presence data into training and testing bins for *k*-fold cross validation. To ensure the best possible model performance, we calculated two additional evaluation metrics recommended for presence-only models. First, the Boyce index indicates the extent to which model predictions differ from random distribution of the observed occurrences (Boyce et al., 2002). This index varies between − 1–1, where positive values suggest that observed predictions are consistent with the distribution of presence in the evaluation dataset, and models with an index close to 1 are considered as the best performing models (Hirzel et al., 2006). Second, the Mean Absolute Error (MAE) represents the mean absolute difference between model predictions and target value (Konowalik and Nosol, 2021). The jackknife procedure and the heuristic method provided by
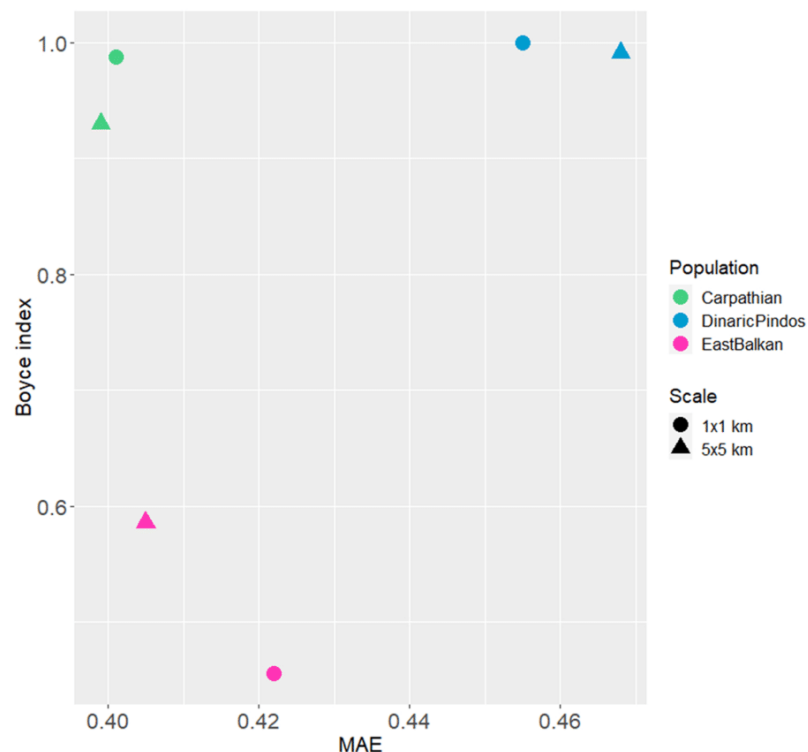
Fig. 3. Model performance based on Boyce index (showing the extent to which model predictions differ from random distribution of the observed occurrences) and Mean Absolute Error (MAE, mean absolute difference between model predictions and target value) values for three brown bear metapopulations (depicted in different colors) at different spatial scales (depicted in different shapes) for bear occurrences gathered in Serbia between 2007 and 2021.

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MaxEnt were used to assess the relative importance of the environmental variables as the proportional contribution of each variable to the model (Phillips et al., 2006).

2.6. Connectivity analysis

To identify potential connectivity areas between populations, we performed landscape resistance analysis following Mateo-Sánchez et al. (2014). We created a landscape resistance surface which reflects how difficult it is for an animal to move through a location (observed as a cell in a raster map) as a function of its environmental features (Adriaensen et al., 2003; Mateo-Sánchez et al., 2014). From the combined model, we obtained the predicted habitat suitability value for each cell in our study area (Phillips et al., 2006), and defined landscape resistance as the inverse function of this value according to the formula $(R`/R`min)^2$, where $R`$ is 1-HS (HS: habitat suitability value for each cell) and $R`min$ is the minimum value of 1-HS across the entire study area (Mateo-Sánchez et al., 2014). As a result, we obtained a unique resistance value for each cell (i.e., the cost of crossing it), where the lowest resistance values match the most suitable habitats.

3. Results

3.1. Model evaluation and variable contribution

Our results showed that two of three population models performed well in predicting habitat suitability. Specifically, the Dinaric-Pindos and Carpathian population models showed high reliability, while the East-Balkan model showed poor predictive ability at both spatial scales (Boyce index of 0.586 and 0.456, respectively), likely due to the small sample size (15 and 25 presence grids, respectively) (Fig. 3; Table S1). We therefore, removed this model from further analyses. In general, altitude and forest were the most important variables determining bear habitat suitability (Table 2).

Dinaric-Pindos population: The best performing model at the coarse scale (5 ×5 km) had a Boyce index of 0.98 and MAE of 0.466, and the fine scale model had values of 1 and 0.458, respectively. These values indicate high quality predictions (Fig. 3; Table S1). The best performing model at both scales had mean AUC values of 0.910 and 0.937, respectively, indicating a high accuracy in distinguishing suitable from unsuitable bear habitats (Table S1). The variables contributing most to the coarse scale model were altitude (63%, Table 2), followed by percentage of forest cover, and distance to first- and third-order roads (Table 2). The other remaining variables had a negligible contribution (Table 2). For the fine scale (1×1 km) model, altitude was the most important variable for habitat suitability (69%, Table 2). Other variables had only minor contributions (Table 2).

Carpathian population: The best performing model at the coarse scale had a Boyce index of 0.93 and MAE of 0.399, while the fine scale model had values of 0.988 and 0.401, respectively (Fig. 3; Table S1). The best performing model had a mean AUC value of 0.850 at the coarse scale and 0.960 at the fine scale (Table S1). Percentage of forest cover (64%, Table 2) was identified as the most important variable on the coarse scale. The variables percentage of scrub cover, altitude, and distance to first-order roads had moderate contributions (16%, 7% and 6%, respectively; Table 2), while the contribution of the remaining variables was negligible. In comparison, the fine scale model was most affected by altitude (38%) and the percentage of forest cover (37%, Table 2), while % of scrub cover and distance to primary roads had moderate contributions (8% and 6%, respectively, Table 2).

Table 2
Variable contribution for coarse (5×5 km) and fine scale (1 ×1 km) models that predict habitat suitability for the Dinaric-Pindos and Carpathian brown bear metapopulations in Serbia. Darkest colors refer to maximum (orange) and minimum (blue) variable importance.

Scale	5km		1km	
Population	Dinaric-Pindos	Carpathian	Dinaric-Pindos	Carpathian
Altitude	63	7	69	38
Forest	11	64	4	37
Scrub	2	16	1	8
Pasture	0	2	0	0
Infrastructure	2	0	0	0
Dist. Water	0.6	4	8	4
Dist. Urban	4	0.3	1	4
Dist. Road1	6	6	6	6
Dist. Road2	5	0.1	5	2
Dist. Road3	7	1	6	1

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3.2. Habitat suitability

To define which habitats are suitable for all bear populations as well as areas that could promote population connectivity, we used a common model based on the highest prediction values from the Dinaric-Pindos and Carpathian models for each grid at both scales. We excluded the Eastern Balkan model from this analytical step due to its poor predictive ability (Fig. 3; Table S1). Suitable habitats were predicted using a threshold (mean predicted suitability for all confirmed presence cells) of 0.57 for coarse scale and 0.58 for the fine scale, i.e., all areas with values higher than this threshold were treated as suitable for bears. At the coarse scale, the common model identified a total of 9400 km^2 (11.5% of the territory of Serbia) as suitable bear habitat, mostly in the southern half of the country (Fig. 4, left panel; Table 3). Based on the presence data, bears occupy 7.6% of the total territory of Serbia, which equivalents to 35.4% of the identified suitable habitats (Table 3). This leaves a substantial portion of suitable habitats (6075 km^2) available for potential population expansion. The fine scale model (1×1 km) predicted a smaller area of suitable habitat (4451 km^2; 5.1% of the entire study area), of which 24.4% is already occupied by bears (representing 2.4% of the entire area of Serbia). Results at both scales indicate that about 60% of current bear occurrences appear within protected areas (Fig. 4, right panel; Table 3).

3.3. Connectivity

Our coarse scale model predicted habitat suitability values ranging from 0 to 0.88, which resulted in resistance values ranging from 0.9 to 59 (Fig. 5). The landscape resistance map at the coarse scale predicted several areas feasible to connect suitable habitats, especially in the southern part of the country. For the fine scale model, habitat suitability values ranged from 0 to 0.94, which resulted in resistance values ranging from 0.9 to 204 (Fig. 5). The fine-scale results indicate that predicted connectivity areas in the south-east are not continuous but suggest potential corridors for the connection between the three bear populations. The Radan Mountain is the only protected area that lies within this potential connectivity area, highlighting its importance as a 'stepping stone' for the connection between European metapopulations (Fig. 5). In addition, our results suggest several potential barriers for bear movement from west to east due to transportation infrastructure, especially a highway in the southeast (Fig. 5).

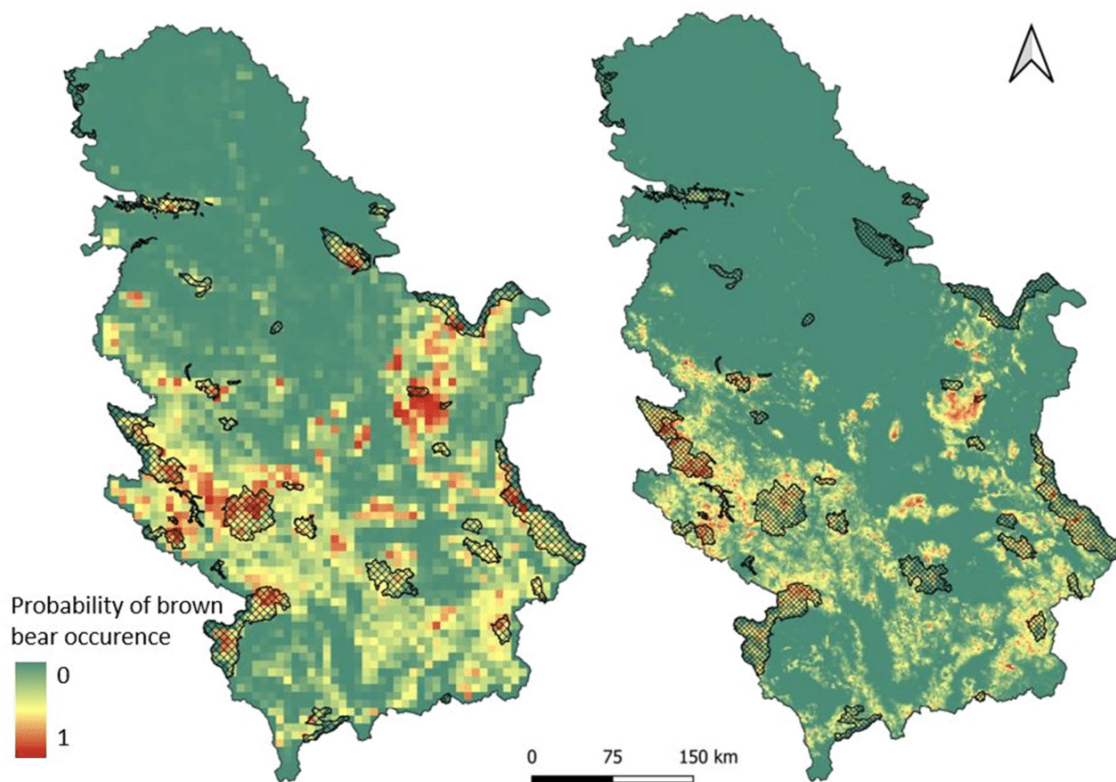**Fig. 4.** Common Maxent models predictions of habitat suitability for brown bears in Serbia (based on data from the Dinaric-Pindos and Carpathian metapopulations) at a coarse (5 ×5 km, left) and fine scale (1 ×1 km, right). Hatched areas depict protected areas in Serbia. Predictions represent the probability of bear occurrence scaled from unsuitable (0, green) to most suitable habitats (1, red).

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Table 3

Area and proportion of predicted unsuitable and suitable, occupied and unoccupied, and habitats inside and outside of protected areas for brown bears in Serbia at different spatial scales (5 ×5 km and 1 ×1 km) in Serbia. Numbers in parentheses with * refer to threshold values above which habitats were considered as suitable.

Categories	Common model			
	5×5 (0.57 *)		1×1 (0.58 *)	
	Area	%	Area	%
Suitable	9400	11.5	4451	5.1
Unsuitable	72,550	88.5	82,574	94.9
Total	81,950	100	87,025	100
Suitable occupied by bears	3325	35.4	1088	24.4
Suitable unoccupied	6075	64.6	3363	75.6
Total	9400	100	4451	100
Suitable occupied inside protection area	2075	62	602	55.3
Suitable occupied outside protection area	1250	38	486	44.7
Total	3325	100	1088	100

4. Discussion

The main goal of this study was to evaluate bear habitat selection at the intersection of three European metapopulations with the long-term goal to establish connectivity between these populations. We found that altitude and forest cover are the most important factors in bear habitat selection; however, there were differences in how bears from the different populations responded to their environments. Our results further show the availability of areas suitable for population expansion as well as highlight especially one area in south-eastern Serbia where functional connectivity between populations could be established. The results show that higher altitude areas and dense forests cover play an important role in brown bear distribution, and that the probability of bear presence at both analytical scales was negatively affected by human infrastructure. These results are consistent with previous results on bear habitat selection (e.g., Jerina et al., 2003; Posillico et al., 2004; Martin et al., 2012; Zarzo-Arias et al., 2018; Almasieh et al., 2019; Ahmadipari et al., 2021). In addition, our models revealed that the underlying drivers of bear habitat selection slightly differed between our studied populations, especially at the coarse scale. This is primarily due to the differences in the habitats available to each population in Serbia. Altitude best explained bear occurrence in the Dinaric-Pindos population, with most occurrences in areas > 1000 m. In comparison, forest cover was the most influential environmental variable for the Carpathian population. These differences are related to the generally higher altitudes in the Dinaric Mountain Range (west and southwest) compared to altitudes in the Carpathian Mountain Range (east) in Serbia. Furthermore, previous studies on brown bear habitat selection showed that bears avoid areas with high human disturbances (Nellemann et al., 2007; Zarzo-Arias et al., 2018; Almasieh et al., 2019; Morales-González et al., 2020). In general, human presence is lower at higher altitudes, which likely is the reason why bear habitat selection in the Dinaric-Pindos population was primarily driven by altitude. On the other hand, due to the lower altitudes in the east of Serbia, bears in these areas occupy more forested areas, which also provide shelter from human disturbances (Martin et al., 2010; Ordiz et al., 2011). Given that bear behavior is influenced by a wide range of environmental (Nazeri et al., 2012; Zarzo-Arias et al., 2018; Zeller et al., 2019) but also population factors (both intra and inter-specific interactions; Nellemann et al., 2007; Ordiz et al., 2020; García-Sánchez et al., 2022), there might be additional factors not considered in our analyses which may also influence bear habitat preferences.

We found that suitable areas predicted at the coarse spatial scale were almost twice the size compared to the fine spatial scale (9400 km^2 vs 4451 km^2; Table 3). This can be related to the fact that the bear is a highly mobile species that usually reacts to the environment at large spatial scales (Mateo-Sánchez et al., 2014, Zarzo-Arias et al., 2018) leading to large areas being predicted as generally suitable. However, habitat use on finer scales may better reflect preference or avoidance of certain habitat features, which are expressed by fine scale movement decisions by bears. Mateo-Sánchez et al. (2014) suggested that topography and human factors were the main drivers of habitat suitability for bears at larger scales, while results at finer scales relate more to variables associated with habitat configuration and edge effects.

Our results provide information about possible directions of bear population expansion (primarily in western, eastern and south-eastern areas of Serbia), which suggests that adequate management measures should be put in place before bears start occupying these areas and conflicts typical for this area start occurring. Our results further show that a considerable portion (~6000 km^2 and ~3000 km^2 at coarse and fine scale, respectively) of habitat predicted as suitable is available for bear populations to increase in size and range. However, most of these areas are fragmented by roads, which pose a threat for connectivity if bears avoid crossing roads or are regularly killed when attempting to cross them (Proctor et al., 2012; Straka et al., 2012; Mateo-Sánchez et al., 2014). Therefore, the main focus of mitigation measures should be to improve habitat permeability and connectivity between fragmented habitat patches, allowing undisturbed movement of animals with large home ranges, such as brown bears.

More than half of the occupied suitable habitats are located inside protected areas, which shows a good overlap between the protected area network and the current bear distribution. Bears tend to avoid human activities both spatially and temporally (Martin et al., 2010; Ordiz et al., 2013; Hertel et al., 2016). Given that human activities are generally limited in protected areas, they could function as important refuges (or stepping stones for connectivity) for bears and other species (Worboys et al., 2010). However, there are also plenty (~35%) of habitats predicted as suitable outside of protected areas, especially in the southwest (around Zlatibor, Zlatar, Jadovnik and Golija protected areas) and the east of the country (around Južni Kučaj protected area). Potential expansion of the

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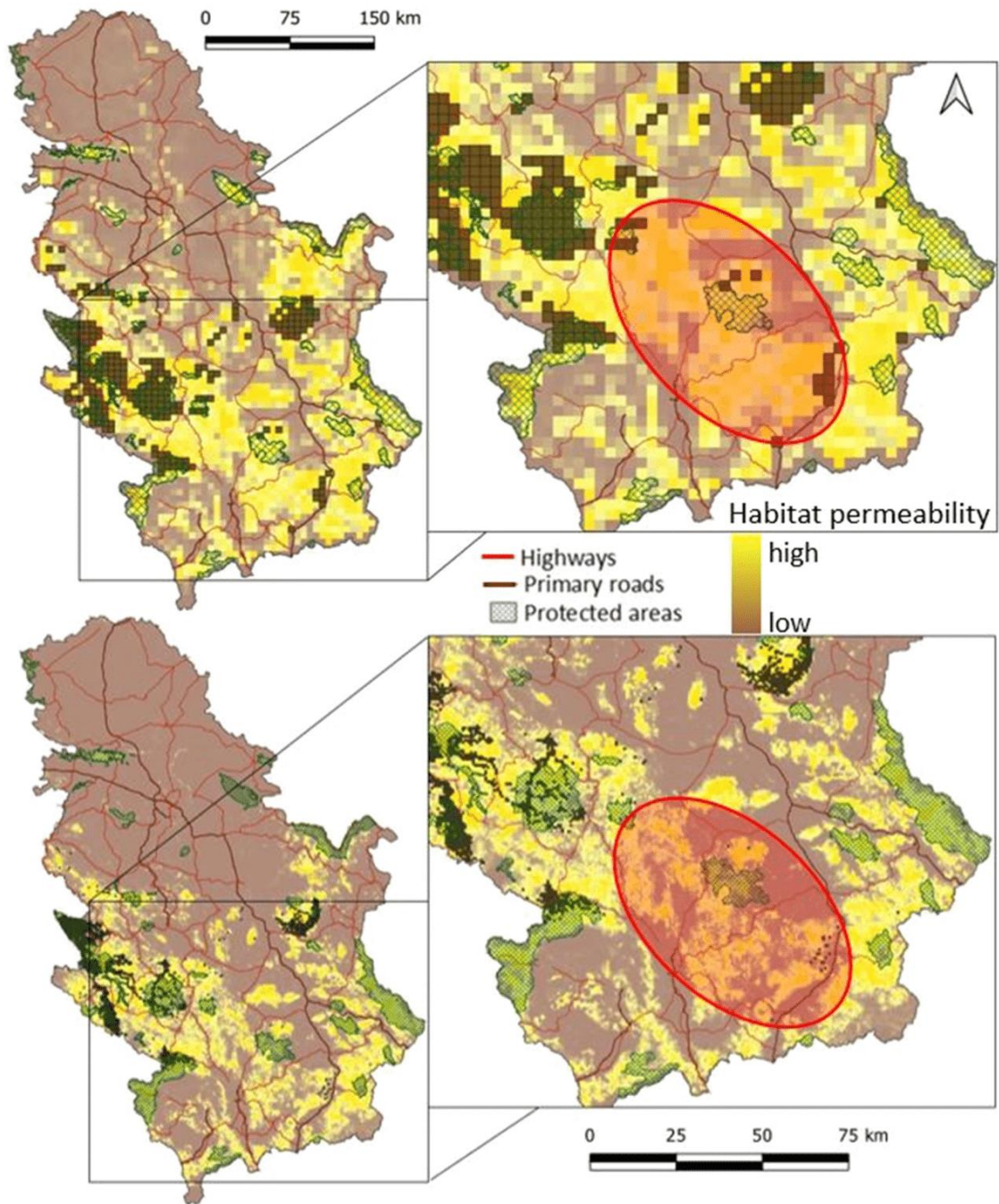
Fig. 5. Landscape resistance maps showing the areas of potential connectivity (red circle) between three European brown bear metapopulations (brown squares depict bear occurrence data) in Serbia. The upper map shows results at a coarse (5 ×5 km) spatial scale, and the lower map results at a fine (1 ×1 km) scale. Areas with lowest resistance values and thus highest permeability for bears are shown in yellow. Green hatched areas depict protected areas in Serbia.

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protected areas network in Serbia could consider including habitats important for brown bears, which has been proposed as a good conservation measure in several other regions (Jerina et al., 2003; Nazeri et al., 2012; Mukherjee et al., 2021). The ongoing expansion of the European Union's Natura 2000 network can be particulary important in this regard.Considering that the conservation of bears in Europe must occurr in a human-dominated landscape, their long-term survival depends on their ability to coexist with humans (Zedrosser et al., 2001; Chapron et al., 2014; Morales-González et al., 2020). Our result can be used as a starting point to identify priority areas where appropriate measures need to be put in place before conflicts arise. Furthermore, given the importance of brown bears as an umbrella species for conservation actions, protecting their habitats will also benefit many other endangered species.

Bears in Serbia are at the intersection of three large European bear populations, and therefore crucial to establish gene flow between these populations (Bogdanović et al. 2021). Our results highlight that gene flow is possible in the southern part of the country, which points to the key role of Serbia for long-term conservation of brown bears in Europe. An area especially suitable for connectivity shows good overlap with the „Radan Mountain" Nature Park, which could promote movement of bears from the Dinaric-Pindos population towards the East Balkan and Carpathian populations, and vice-versa. Yet, the habitat permeability analysis revealed that this area intersects with several local and national roads. The major highway, which is located in the central part of the country, will likely represent the most important barrier for bear movement and dispersal, together with the natural terrain formation of the Morava River valley. Numerous studies have shown that roads (Alexander et al., 2005; Riley et al., 2006; Koreň et al., 2011; Mateo-Sánchez et al., 2014) are a major barrier for movement of wildlife, especially fenced highways. These high-volume and high-speed motorways pose a particular threat to species with large home ranges, such as brown bears, leading to a reduction in genetic exchange (McCown et al., 2009; Karamanlidis et al., 2012). Therefore, special attention should be paid to mitigate the effects of these movement barriers. Wildlife underpasses and overpasses combined with road fencing are effective mitigation measures for reducing wildlife-vehicle collision, but also for increasing road permeability for animal movement (Clevenger and Waltho, 2000; Huijser, McGowen, 2010; Huijser et al., 2016; Rytwinski et al., 2016). Given their high costs, such activities must be well designed and placed in the most cost-effective places for species of concern (Kaczensky et al., 2003). Our results can serve as an important guide to highlight the most significant areas where mitigation measures would have the greatest effect on increasing habitat permeability. The rapid expansion of the national transportation network in Serbia, especially the construction of a new highway (Miloš the Great), poses a new serious threat for bear conservation. This highway under construction will pass through parts of the Dinaric-Pindos bear distribution range and prevent the connection with populations to the east (Easter-Balkan and Carpathian populations). In general, a crucial part of all long-term bear conservation programs must be to minimize habitat loss and fragmentation as well as to improve the quality and connectivity of suitable habitats (Swenson et al., 2000; Chapron et al., 2014; Morales-González et al., 2020).

5. Conclusion

Our results are of crucial importance for the long-term conservation of brown bears in Europe, as they highlight the unique possibility to connect three different bear metapopulations in south-eastern Europe. Because bears require large areas of suitable habitat, conservation strategies must focus on preventing further habitat fragmentation and loss as well as on improving connectivity among existing occupied areas (Swenson et al., 2000; Chapron et al., 2014; Mateo-Sánchez et al., 2014; Almasieh et al., 2019; Kouchali et al., 2019). Our results identify areas and landscape corridors important for genetic connectivity between bear metapopulations and provide suggestions for areas in Serbia where connectivity should be improved. Protected areas generally provide suitable habitat for bears but are often too small to support a sustainable population. Our results suggest that improving connectivity between protected areas, despite their small size, could be part of a strategy to improve overall landscape connectivity and habitat suitability that is also beneficial for far-ranging species, such as bears. However, large-scale and long-term conservation of population connectivity must mainly occur in the human-dominated landscape outside of protected areas (Chapron et al., 2014). Therefore, we highly recommend to evaluate current national conservation policies in order to define and appropriately manage landscape connectivity in Serbia as well as in adjacent countries, also by increasing the number and connectivity of protected areas. Furthermore, improving habitat suitability and connectivity for bears will also benefit the long-term conservation of several other species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02460.

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IV DISCUSSION

Although brown bears have always been present in Serbia, research on the species has been carried out only for about 20 years. In the beginning, this research was mainly based on non-invasive sampling (e.g. hair, feces) (Karamanlidis *et al.*, 2014), camera traps and observations of bears and bear family groups. Telemetry studies began in 2007 and to date 30 individuals have been captured and equipped with GPS collars, resulting in over 300,000 GPS fixations. In the first analysis, Ćirović *et al.*, (2015) described the long-distance movement and activity pattern of a single GPS-collared subadult bear. In addition, Serbia contributed with data in a study on large carnivore recovery (Chapron *et al.*, 2014) and more recently in a global study on mammalian responses to COVID-19 lockdown (Tucker *et al.*, 2023). The analyzes in this dissertation are based on 20 collared individuals followed over 1-3 years between 2007 and 2022, making this the first comprehensive study on the movement ecology of brown bears in Serbia. Therefore, the results presented here are an important basis for future national conservation and management strategies.

1. Nocturnality in bears: an advantage for some, but pitfall for others

Spatio-temporal changes in animal space use are often observed as a first response to increasing human disturbance, with bears being no exception (Ordiz *et al.*, 2014, 2017; Gaynor *et al.*, 2018). Thus, in a human-dominated environment, survival strongly depends on a species' capacity to adjust its behavior and cope with human-induced disturbances. In line with the dissertation objectives, the first study provided insight into the temporal variation in movement patterns of 13 GPS-collared brown bears (8 males and 5 females). The results based on the 26 "bear years" (each year in which a bear was monitored) showed pronounced diel and seasonal variations in brown bear movement patterns, which also varied between the different reproductive categories (i.e. adult males, subadult males, solitary females and females with offspring). In general, bears were predominantly active during crepuscular and night hours, which is consistent with other studies (Kaczensky *et al.*, 2006; Ordiz *et al.*, 2013b, 2014; Hertel, Swenson & Bischof, 2017) and confirms the significant influence that human presence can have on bears' diel activity. In addition to avoiding human encounters, temporal niche partitioning in bears also occurs as a strategy to avoid aggressive conspecifics (Ordiz *et al.*, 2014). This strategy is particularly important for younger individuals and females with dependent offspring, as it can increase their survival rate or the survival rate of offspring. The results obtained confirmed this assumption and showed that females accompanied by dependent offspring were more diurnal compared to all other bear classes. In slow-reproducing species with prolonged maternal care, such as brown bears, sexually selected infanticide represents one of the main causes of offspring mortality, especially in the first year of life when their mobility is very limited (Dahle & Swenson, 2003a; Steyaert *et al.*, 2012, 2013). Thus, by shifting their activity to daylight hours, females can ensure easier access to food and increase the offspring safety by avoiding infanticidal, nocturnal males. As mentioned above, human presence represents one of the main causes of nocturnal behavior in most brown bear categories. Therefore, it is noteworthy to say that the lack of negative experiences with humans could be one of the reasons for the higher diurnal activity observed in cubs, which may continue even after weaning. However, unlike in females with dependent offspring, the movement patterns of

weaned bears (i.e. subadults) change primarily to avoid inbreeding and reduce intraspecific resource competition (Kaczensky *et al.*, 2006; Zedrosser *et al.*, 2007b; Parres *et al.*, 2020), even if they face negative human encounters. In contrast to other studies, the results of this dissertation showed no significant temporal niche partitioning between subadult and adult bears, which could be due to the relatively small population size in Serbia, making it less likely that individuals will encounter each other even if they are active at similar times. Despite the low diurnal activity, the subadult bears moved over significantly longer distances than all other categories during the dark hours of the mating season, suggesting dispersal behavior. Therefore, it might be assumed that behavioral flexibility in females with dependent offspring and in subadults emerged primarily as a response to intraspecific social dynamics rather than to human disturbance. In line with this, several studies have shown that vulnerable individuals might perceive humans as less threatening than other bears, leading them to seek protection in the vicinity of humans (i.e. the human-shield hypothesis; Rode *et al.*, 2006; Steyaert *et al.*, 2016a). However, it should be noted that the more frequently bears approach human settlements, the more often human-bear conflicts occur, which in turn could affect bear behavioral patterns. Due to their lower wariness, subadult bears and females accompanied by cubs are most frequently involved in human-bear encounters in Serbia and elsewhere (Kaczensky *et al.*, 2006; Nellemann *et al.*, 2007; Ćirović & Paunović, 2018). Although these encounters very rarely involve human injury, they are sometimes associated with damage to human property (e.g. crops, beehives, livestock), which can lead to the removal of "nuisance bears" (Can *et al.*, 2014; Penteriani *et al.*, 2016). Given that brown bears are recovering and their numbers are increasing in most parts of Europe (Zedrosser *et al.*, 2011; Chapron *et al.*, 2014), it is expected that these conflicts will become even more prominent in the coming years. However, it should be kept in mind that human avoidance may counteract the switch towards more diurnal activity of females with dependent offspring and subadult bears, making them more prone to infanticide or inbreeding. Since it is not possible to completely prevent human intrusion into bear habitats, maintaining and promoting spatial and/or temporal separation between humans and bears is one of the most important prerequisites for future conservation strategies. Such strategies should be based on both raising public awareness of the importance of brown bear conservation and implementing appropriate bear deterrence measures that will reduce and prevent future conflicts.

2. Clustered food resources can reduce movement but improve foraging efficiency in bears

In addition to significant inter-individual variations, the bears in the analyzed area exhibited remarkable inter-seasonal variation in their movement patterns. In general, a significant decrease in movement rates from mating towards hyperphagia season was observed in all bear categories, except for females with dependent offspring. In contrast to other conspecifics, females accompanied by young not only increased their movement, but also shifted their activity to become more crepuscular, probably to compensate for the increased mobility and nutritional requirements of young. During the hyperphagia season, bear behavior is governed by intensive food search, which usually requires less roaming than mate searching or dispersal. However, considering that natural food sources are not clumped but rather scattered within heterogeneous environment, foraging still implies a large movement investment (Ferguson *et al.*, 2001; Blanchet *et al.*, 2020). Conversely, human-

modified environments provide somewhat more reliable and accessible food sources, causing many animals, including bears, to rely on them, thus slowly changing not only their foraging efficiency but also their natural behavior. It is therefore not surprising that bears, whose habitats largely overlap with those of humans, especially in Europe, are shifting their foraging towards more accessible food sources, thereby reducing their movement rates. In addition to the significant spatio-temporal changes in the resources distribution, the intentional provision of food to wildlife (i.e. supplementary or diversionary feeding) also contributes to making food resources even more clustered and predictable (Selva *et al.*, 2014, 2017). Previous studies have shown that bears and other species reduce their movement distances and home range sizes in response to supplementary feeding (Cozzi *et al.*, 2016; Selva *et al.*, 2017; Penteriani *et al.*, 2021). Since bears are omnivores with high nutritional requirements, they will exploit anthropogenic subsides whenever they encounter them, regardless of whether they are intended exclusively for bears or for game species (mostly for wild boars and less for wolves and vultures; Ćirović & Paunović, 2018). Consequently, bears have been shown to reduce their home ranges when the density of feeding stations increases, and often roam less in areas where supplementary feeding is practiced (Cozzi *et al.*, 2016; Selva *et al.*, 2017; De Angelis *et al.*, 2021; Penteriani *et al.*, 2021), which could further promote their higher fidelity to these areas. In addition, Woodroffe, Thirgood & Rabinowitz (2005) have raised concerns about the potential risk of species becoming more habituated to humans, as they may associate supplemental feeding with humans. However, in Serbia, as in many other countries, this practice is not allowed near human settlements, primarily because it can promote disease transmission (Sorensen *et al.*, 2014), but also to avoid wildlife food conditioning (Huber *et al.*, 2008). In general, feeding stations in Serbia aim not only to enhance brown bear population recovery, but also to keep bears (and other carnivores) in desired habitats and thus divert them from approaching human settlements. However, insufficient data on food supplementation regime (i.e. frequency and amount of food provided) along with a large number of unregistered feeding sites (i.e. baiting sites for wild boar) within bear habitats make wildlife management in this area very difficult. Furthermore, the increasing use of automatic feeders, which can easily be moved from one place to another, makes it even more difficult to control the availability of anthropogenic food in the nature. Therefore, further research is needed to reveal how human-provided food subsidies alter brown bear movement ecology and whether we can expect that this practice will promote nuisance behavior in bears.

3. Climate change and supplementary feeding may drive bears out of hibernation

Although not as intensive as in the countries where they are hunted (i.e. Croatia, Slovenia, Bosnia and Herzegovina), bears in Serbia are subject to supplemental feeding (mostly with corn and carrion), which has been used for more than two decades, primarily as a damage control measure. However, despite the positive effects of this long-term practice on local bear populations (according to recent assessments, an increase in bear populations has been observed; Ćirović & Paunović, 2018), the results of the current study also show serious undesirable side effects. In addition to the aforementioned changes in movement patterns that may be further reinforced by this practice, there is growing concern about how these anthropogenic subsidies will affect other aspects of the bear's life cycle. In line with recent findings indicating the potentially negative effects of this practice on bear

hibernation (Kavčič *et al.*, 2015; Štofík *et al.*, 2016; Krofel *et al.*, 2017; Bojarska *et al.*, 2019), this dissertation aimed to show whether and to what extent climate change and supplementary feeding lead to hibernation alterations. Most of the existing literature on the bear hibernation ecology in this part of Europe is mainly based on observational data (tracks, scat, etc.) (Nores *et al.*, 2010; Bojarska *et al.*, 2019). Thus, this study is one of the few based on telemetry data (a total of 20 GPS-collared brown bears) and represents an important contribution to this field. The study revealed great variability across the 31 winter events, with significant inter-individual but also intra-individual variations, where the same individual showed different winter behaviors in consecutive years. In general, the results revealed 6 events with a single hibernation period, 19 events where hibernation was interrupted (up to 4 times) for short periods, and 6 events inconsistent with hibernation where bears remained partly or completely active during winter. Among the bears in which hibernation was observed, its onset, duration and emergence varied markedly depending on the sex and reproductive status of the bear, although the general pattern was that females spent significantly more time hibernating compared to males, as has been shown elsewhere (Manchi & Swenson, 2005; Pigeon *et al.*, 2016; Krofel *et al.*, 2017; González-Bernardo *et al.*, 2020). The study also confirmed that females with cubs of the year (i.e. they entered den pregnant and left with cubs) were the first to enter and the last to leave the den. Prolonged hibernation could therefore be necessary for the reproductive success of females. However, the results revelaed that one old male (estimated age over 10 years) spent 138 days in the den, which is longer than hibernation length observed in solitary females and females with dependent offspring. As this is an isolated case, it must be interpreted with caution, and highlights the need for further research to fully understand brown bear hibernation behavior in the study area. Furthermore, it has been suggested that the pronounced global warming together with the human-provided food leads to changes in the bears' winter behavior. So far, areas with mild winters and/or prolonged natural food availability have often been associated with shortened, interrupted or even skipped hibernation in brown bears (Van Daele *et al.*, 1990; Linnell *et al.*, 2000; Nores *et al.*, 2010). However, recent studies have initiated an intense debate about the potential impacts of climate change and supplementary feeding on bear hibernation (Pigeon *et al.*, 2016; Krofel *et al.*, 2017; Delgado *et al.*, 2018; Bojarska *et al.*, 2019; González-Bernardo *et al.*, 2020). In line with this, the current study revealed partial or complete absence of hibernation in 6 winter events, exclusively displayed by males (3 adults and 3 subadults). In particular, three individuals showed semi-active behavior with stationary periods of 1-26 days, while the other three individuals showed no signs of stationary behavior and moved throughout the entire winter. All winter-active bears repeatedly visited known supplementary feeding sites, suggesting their great importance during the winter months (according to the results, bears spent ~50% of their time near the feeding sites in January). It can therefore be assumed that a higher fidelity to the feeding sites during winter in the study area is associated with a hibernation alteration, causing the bears to shorten or forgo hibernation. Furthermore, in Slovenia, where bears have been intentionally fed for over 100 years, Krofel *et al.* (2017) found that the expected duration of hibernation (~130 and ~150 days for males and females, respectively) decreased by 45-56%, while the use of feeding sites increased remarkably (by ~60% compared to the non-hibernating period) in bears that were outside the den during winter period. Thus, it should be expected that intentional food provisioning during the winter months can trigger profound negative consequences for hibernation behavior if the bears become habituated to these food sources. Similar assumptions have been proposed for other bear populations where supplementary feeding has been practiced over a longer period of time (Selva *et al.*,

2017; Bojarska *et al.*, 2019; González-Bernardo *et al.*, 2020). In addition, Fagan *et al.* (2013) have shown that memory could play a very important role in animals' movement decisions by allowing them to reduce uncertainty regarding their position in relation to a specific location (spatial memory) or its characteristics (attribute memory). By memorizing valuable locations (food-rich places, shelter or den sites, mating areas), animals can choose between alternative paths in the environment, thus reducing their time and energy expenditure while increasing their fitness (Fagan *et al.*, 2013). Although no precise information on the frequency of food provisioning was available, the GPS data together with the camera trap data (the camera traps operated year round at the bear'-intended feeding stations) indicated that bears regularly visited these sites even when no food was available. It is therefore assumed that the bears have memorized these sites and probably visit them whenever natural food sources are depleted or when they are nearby. In addition to food availability, climatic variables, especially ambient temperature and snow cover, are considered one of the main triggers for the onset of hibernation in brown bears (Manchi & Swenson, 2005; Evans *et al.*, 2016; Pigeon *et al.*, 2016; Krofel *et al.*, 2017; Bojarska *et al.*, 2019). Although most of the analyzed bears exhibited some type of hibernation behavior, some individuals remained active despite the cold weather conditions. However, their movement rate decreased with increasing snow depth (from 2.5 km/day when there was no snow to 1.1 km/day in 50 cm deep snow), probably as a trade-off to save energy. Thus, the obtained results show that individuals exposed to the same environmental conditions may choose different overwintering strategies, thereby implying within-population hibernation plasticity. Although the results are based on a relatively small sample size, they suggest that human-induced environmental changes, in particular the increasing availability of food, may favor the coexistence of different hibernation strategies: obligate hibernation in females with offspring of all ages, facultative hibernation throughout the winter, facultative intermittent hibernation and active overwintering. Considering that bears are facultative hibernators, where hibernation only occurs when environmental conditions become too harsh to maintain a constant body temperature, it should be expected that increasing winter temperatures along with prolonged food availability (both natural and anthropogenic) will lead to more active bears in winter, at least in males. However, as females give birth while in hibernation, it is even more urgent to understand how these changes might affect their fecundity but also the survival of cubs. Climate warming and human activities have and will continue to alter both the appearance and conditions of the world's ecosystems. It is therefore expected that non-hibernating individuals will become a more ubiquitous phenomenon in the following decades.

4. Protected areas can act as refuges for bears but also steppingstone for landscape connectivity

Like the rest of Europe, Serbia is undergoing intensive infrastructure development (e.g. expansion of the highway and railroad network), which is accompanied by immense human intervention in wildlife habitats. Over the last two decades, significant changes in land use combined with rapid development of transportation infrastructure have altered the appearance of many habitats. According to recent estimates, more than half of the country's surface (~54%) has undergone some degree of human-caused alterations, with ~33,000 km² (37% of the country's surface) converted to heavily managed agricultural land (MCTI, 2021). Although bears in Serbia are mostly found in remote, sparsely populated,

forested areas, the above-mentioned environmental changes have severely affected their populations and caused the bears to modify their natural behavior. Due to the lack of knowledge regarding bear habitat selection in Serbia, the aim of this dissertation was to evaluate whether and to what extent human-induced habitat alterations affect bear habitat selection in each of the three populations, and to predict suitable habitats into which bears could potentially expand. In contrast to the other two studies, which relied solely on telemetry data, this study also included bear occurrence data, such as scat, footprints, hair, but also camera-traps data. The results of habitat suitability modeling for the Dinaric-Pindos and Carpathian populations showed that the presence of bears is negatively associated with human infrastructure, while the bears preferred higher elevations and forested areas. Considering that these populations are exposed to different topography, land cover and human disturbance, the results confirmed significant differences in the way the bears from these two populations responded to their environment. In particular, bears in western and southwestern Serbia were mostly found in areas above 1000 m indicating the great importance of altitude for Dinaric-Pindos bears. On the other hand, bears in the eastern part of the country, which is much lower (highest point 1339 m compared to 2656 m in the southwest), were much more dependent on dense forested areas. The results confirmed that in both populations, bear habitat selection was predominantly driven by human avoidance, with bears mostly choosing high-altitude, remote and inaccessible terrains characterized by low levels of human disturbance. This is consistent with previous studies on bear habitat selection, which have shown that increased human density reduces habitat quality, which in turn can have severe negative consequences for bear populations (i.e. spatio-temporal behavioral changes, lower reproductive success, frequent human-bear encounters; Linnell *et al.*, 2000; Nellemann *et al.*, 2007; Martin *et al.*, 2010; Zarzo-Arias *et al.*, 2019; Morales-González *et al.*, 2020). According to the latest estimates, all three bear populations in Serbia are increasing in size (the fastest growth rate is observed for the Dinaric-Pindos population; Ćirović & Paunović, 2018), and this trend is expected to continue in the coming years. Identifying suitable habitats into which bears can expand their current range is therefore a keystone on which national conservation strategies should be built. The study found that more than 60% of the predicted suitable habitat for bears is still available, both at the coarse and fine scale (~6000 km^2 and ~3000 km^2, respectively). Furthermore, the results confirmed that the current distribution of bears largely corresponds to the network of protected areas (more than half of the bear occurrences are located in protected areas). These results indicate the great importance that protected areas can have for the long-term survival of brown bears, as they can serve as refuges since human activities are relatively restricted within these areas. Previous studies have discussed the benefits of expanding or even establishing new protected areas to encompass habitats important for bears (Jerina *et al.*, 2003; Nazeri *et al.*, 2012), which can also be considered one of the very useful conservation measures in Serbia. Furthermore, bears are listed as Natura 2000 species (European Commission, 1992). Therefore, predicting which habitats are most suitable for them could be of great importance for the designation of the European Union's Natura 2000 network which is currently being developed in Serbia. Considering the main focus of Natura 2000 (i.e. the long-term survival of the most valuable and threatened species and habitats in Europe) implementing results of this study into Natura 2000 activities can significantly contribute to the conservation of the brown bear in Serbia. However, protected areas are often very limited in their size and therefore cannot sustain viable brown bear populations. Instead, as bears are expanding towards more human-modified landscapes, appropriate management and conservation strategies must also be applied outside protected areas, where establishing human-bear

coexistence is crucial for the long-term survival of bears. In addition to the higher probability of encountering humans in such environments, bears in highly fragmented landscapes face reduced habitat permeability and connectivity. Under such conditions, the movement of individuals is restricted and can lead to a reduction in gene flow, thereby obstructing population connectivity (Mateo-Sánchez *et al.*, 2014; Skuban *et al.*, 2017). Therefore, the identification of suitable habitats and key movement corridors is crucial for establishing functional connectivity, as it can indicate areas where conservation measures need to be prioritized. Serbia is the only European country where three different European bear populations meet and can therefore have a significant influence on the long-term conservation of brown bears in south-eastern Europe. In particular, its geographical position gives Serbia a unique opportunity to establish and maintain long-term connectivity between these populations. Although connectivity between the three bear populations in Serbia has not been documented, the results of this study predict several areas in the southern and south-eastern part of the country where gene flow could be established in the future. The only protected area here is the "Radan Mountain" Nature Park, where movements between Dinaric-Pindos, Carpathian and Eastern Balkan bears are most likely to occur. Like the rest of Serbia, this area has undergone significant human-caused alterations, mainly due to the development of road infrastructure. Therefore, the major highway and railroad (connecting the northern and southern parts of the country) together with the local terrain topography (Morava River valley) and high population density are likely to be a major barrier for bear movement. Negative ecological impacts of roads, but also railroads, on bear behavior, reproduction and viability have been reported throughout the entire brown bear's distributional range. By reducing habitat permeability, roads can alter the movement patterns of bears (Karamanlidis *et al.*, 2012; Mateo-Sánchez *et al.*, 2014; Bischof *et al.*, 2017; Penteriani *et al.*, 2018), making it much more difficult for them to find food or mating partners. In addition, reduced population connectivity can seriously affect genetic diversity, as isolated populations become more susceptible to inbreeding depression (Morales-González *et al.*, 2020). Besides, bears can be killed in vehicle collisions (Krofel, Jonozovič & Jerina, 2012), which in case of human injuries might further intensify human-bear conflicts. Therefore, future management efforts should focus on mitigating movement barriers and improving habitat permeability. In particular, fencing of high-volume and high-speed motorways along with wildlife crossing structures (underpasses, overpasses, open-span bridges) can help to ensure genetic exchange and maintain functional connectivity (Ford, Barrueto & Clevenger, 2017; Morales-González *et al.*, 2020). Considering that the Spatial Plan of the Republic of Serbia foresees large investments in the development of transport infrastructure in the coming years, it is expected that habitat permeability, and thus connectivity will continue to decrease (MCTI, 2021). The results of this study can therefore be used by authorities to make informed decisions and take appropriate mitigation measures in the places that are most cost-effective for the conservation of bears. As bears in Serbia are slowly increasing in both number and range, it will no longer be possible to keep them outside of human-dominated habitats. Therefore, despite the great importance that the expansion and designation of protected areas could have for brown bear conservation in Serbia, such measures may not be sufficient in the long term. Future management efforts must therefore aim to improve the quality and connectivity of human-modified landscapes while adapting human activities to promote the coexistence of bears and humans.

V CONCLUSIONS

In accordance with the main objectives of the dissertation and the results obtained, the following main conclusions can be drawn:

- The nocturnal activity of brown bears is primarily a response to increasing human disturbance, although significant within-population and seasonal variations were observed.
- Females with dependent offspring and subadult males modify their movement patterns (i.e. become more diurnal or disperse) in response to male conspecifics, ultimately to avoid infanticide or inbreeding.
- All bear classes, with the exception of females with dependent offspring, reduce their movements during hyperphagia compared to the mating season, and intentional food provisioning (i.e. supplementary feeding) probably plays a very important role in shaping the brown bear movement ecology in this study area.
- The hibernation chronology varies between bears of different sexes and reproductive categories, with males spending significantly less time hibernating compared to females. Among females of different reproductive status, females with cubs of the year are the first to enter the den and the last to leave, followed by females with yearlings and then solitary females.
- Climate change and the increasing availability and predictability of both natural and anthropogenic food resources alter brown bear hibernation behavior.
- Year-round supplemental feeding facilitates the existence of four different overwintering strategies: obligate hibernation in females with dependent offspring of any age, single facultative hibernation, facultative intermittent hibernation with one or more short stationary periods, and complete activity.
- Due to the different orography and land cover in western and eastern Serbia, bears belonging to different populations showed distinctive habitat preferences, with altitude being the most important factor in habitat selection of Dinaric-Pindos bears, while forest cover better explained the occurrence of bears in the Carpathian population.
- More than 60% of the predicted suitable habitat in Serbia is still available for bear populations to increase in size and range.
- Protected areas play an important role in brown bear habitat selection, as more than half of the bear occurrences are located within these areas.
- The south-eastern part of Serbia, in particular the "Radan Mountain" Nature Park, represents a possible area where a functional connectivity between three populations could be established in the future, but appropriate mitigation measures need to be implemented.

As the first comprehensive study on the ecology of brown bears in Serbia, the results of this doctoral dissertation confirm the significant impact of human-induced environmental changes on the species' behavior. As these changes are expected to be even more pronounced in the coming decades, the results presented here are crucial for the evaluation of current management policies and the direction of future conservation efforts that could greatly benefit the long-term survival of brown bears not only in Serbia, but also in Europe.

VI LITERATURE

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Appendices

Biografija autora

Neda Z. Bogdanović je rođena 25.11.1994. godine u Kraljevu. Osnovnu i srednju Poljoprivredno-hemijsku školu u Kraljevu završila je sa odličnim uspehom. Biološki fakultet Univerziteta u Beogradu, studijski program Opšta biologija upisala je školske 2013/2014. godine, a diplomirala je 2017. godine sa prosečnom ocenom 9,79. Iste godine nastavlja master akademske studije na Biološkom fakultetu, studijski program Biologija, modul Zoologija koji završava sa prosečnom ocenom 10 odbranom master rada „Procena uticaja saobraćajne infrastrukture na populacije vodozemaca i gmizavaca na području Obedske bare (Vojvodina)". Nakon završenih master studija, školske 2018/2019. godine upisuje doktorske studije na Biološkom fakultetu, studijski program Ekologija, modul Zaštita biodiverziteta. Od februara 2019. godine Neda Bogdanović je zaposlena na Katedri za ekologiju životinja i zoogeografiju, Biološki fakultet Univerziteta u Beogradu kao istraživač pripravnik na projektu „Enzootski transmisioni ciklusi patogenih mikroogranizama" koji je finansiran od strane Ministarstva prosvete, nauke i tehnološkog razvoja Republike Srbije (173006). Zvanje istraživača saradnika stekla je u novembru 2022. godine. Neda Bogdanović je bila član velikog broja nacionalnih projekata, a trenutno je član projekta „PARASITE_HUNTER, Environmental Monitoring of Food and Waterborne Parasites" u okviru programa PRIZMA, Fonda za nauku Republike Srbije. Autor je ili koautor 10 naučnih radova u međunarodnim vodećim časopisima iz M20 kategorije (dva M21a, tri M21, četiri M22, i jedan M23) i 11 saopštenja na skupovima međunarodnog značaja, štampana u celini ili izvodu.

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