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# Dietary habits of the brown bear (*Ursus arctos*) in the transboundary Prespa basin

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## Abstract

Proper conservation of large carnivores always entails a robust understanding of their ecology. The diet is one of the fundamental elements that needs to be well assessed before proposing sound management measures. The brown bear population in Prespa is shared among three countries – Albania, Greece and North Macedonia – that considerably vary in habitat complexity and the human practices taking place. Therefore, a comprehensive evaluation of the bear's dietary habits is essential to minimize potential human-bear conflicts. To that aim, a total of 553 samples were collected from 22 different habitats in all three countries. The results indicate that the diet of bears greatly depends on fruiting plants, with cherry plums (*Prunus cerasifera*) present in nearly half of the samples. The seasonal availability of fruits and plants also plays a crucial role, where grasses and early bloomers, like wild cherries, are more dominant in spring, cherry plums in summer, while apples and hardy masts, like acorns, predominate in autumn. In addition, results show that predation and scavenging play an insignificant role in the diet of this subpopulation of bears, with mammal remains detected in 4.7% of the samples, and only 1.45% of which belong to livestock, rendering the bear a less likely threat to livestock farming in the area. One cannot exclude the potential threat bears pose to agricultural activities, although its extent is still unknown. Thus, future conservation and management plans in Prespa should consider the dietary habits and habitat preferences of the brown bear.

**Keywords**: trophic niche, feeding ecology, scat analysis, Prespa, large carnivore management

## Introduction

Large carnivores are an indispensable component of a healthy ecosystem. They play a pivotal role in maintaining the populations of large herbivores, acting as the ecosystem's regulatory system, keeping it in balance (Hoeks et al. 2020). Understanding their diet is vital, in order to design sound conservation and management measures to ensure cohabitation with them and to lessen any potential human-wildlife conflicts (Treves and Karanth 2003; Manfredo and Dayer 2010; Krofel et al. 2020).

Even though they are taxonomically considered carnivores, in an ecological sense, brown bears are omnivorous (Coogan et al. 2018; Swenson et al. 2020). Moreover, they are regarded as one of the most opportunistic omnivores in the animal kingdom, whose dietary choices encompass the widest variety of foods (Kavčič et al. 2015; Coogan et al. 2018). A clear north-south gradient is present in terms of bear diet variation (Bo-

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jarska and Selva 2012), with diet at higher latitudes being more meat-based, such as in Scandinavia (Dahle et al. 1998; Persson et al. 2001), and more plant-based in the south (Cicnjak et al. 1987; Paralikidis et al. 2010). Active predation typically requires more energy and it poses a higher risk since bears are not efficient hunters and usually prefer scavenging rather than actively chasing their prey (Elgmork and Tjørve 1995; Mattson 1997). Occasionally, however, bears are known to hunt and kill weakened, neonate or subadult ungulates (Swenson et al. 2007). Numerous research (Berducou 1983; Elgmork and Kaasa 1992; Clevenger et al. 1992; Paralikidis et al. 2010) shows that brown bears depend on the current availability of foods and usually opt for the food items that are easily accessible, such as fruits and other edible plant parts that are in season.

The Prespa region, a biodiversity hotspot (Schwaderer and Spangenberg 2009), is home to many fruiting species readily available to the brown bear. Since it is also a human-populated area, with agriculture and animal husbandry as the main sources of livelihood, it was crucial to assess the dietary habits of the bear in order to avoid and prevent any conflicts with humans. Moreover, being a transboundary area shared by three countries – Albania, Greece and North Macedonia – it is necessary to evaluate the influence that the vastly different management practices have on the feeding behaviour of this large carnivore.

Past efforts to estimate the diet of brown bears in Prespa, done in the mid-to-late nineties (Mertzanis et al. 2000), have concluded that hard masts and *Prunus* fruits are principal dietary choices for brown bears. Much of the previous work done on this large carnivore in the region (e.g. Melovski et al. 2008; Trajce et al. 2008) has led to the development of a Conservation Action Plan (Stojanov et al. 2012), summarizing the brown bear status as well as proposing recommendations for future studies. Our study therefore intends to update and further advance the knowledge of brown bear diet in the complete Prespa basin, as well as to provide insights into their habitat preference, movement and behaviour.

The questions that this paper strives to answer are related to the dietary habits of the brown bear in the Prespa region, how it affects human activities in the area (agriculture and animal husbandry) and whether it incites any bear-human conflicts (Trajce et al. 2021).

## Materials and methods

### *Study area*

Prespa is a cross-border basin shared among Albania, North Macedonia, and Greece (Figure 1). The basin is composed of two ancient lakes (Lesser Prespa Lake, 43 km$^2$, and Great Prespa Lake, 259 km$^2$) and has exceptional natural value, which is why it is considered a conservation hotspot. The wider Prespa region encompasses 1386 km$^2$, featuring nearly 60 habitat types (Vrahnakis et al. 2011; Fotiadis et al. 2018, 2020). Around 60 mammal species are met in the basin, among which are the brown bear (*Ursus arctos*), grey wolf (*Canis lupus*), chamois (*Rupicapra rupicapra balcanica*) and the critically endangered Balkan lynx (*Lynx lynx balcanicus*) (Stojanov and Hoxha 2021). Sporadic presence of the golden jackal (*Canis aureus*) has also been recorded (Catsadorakis et al. 2021). The region is also inhabited by 26 bat species, making it one of the areas with the highest diversity of bats in Europe (Papadatou et al. 2011). This rich diversity justifies the existence of one national park in Albania, one in Greece, and two national parks and one nature park in North Macedonia, essentially making Prespa one of the largest cross-border protected areas in Europe (Vasilijevic and Pezold 2011).

The wider Prespa area is home to 5,000 people in the 12 villages in Albania, 14,500 in the 38 villages and one town in North Macedonia and 1,500 in the 13 villages of Greece. Most of these people are employed in the primary sector, with intensive bean farming in Greece and vast monoculture apple plantations in North Macedonia. In Albania, this region is more underdeveloped, with the main income for the locals coming from tea production and other mixed cultures. Eco-tourism is increasingly becoming more popular, especially in Greece and North Macedonia.

### *Fieldwork methodology*

The fieldwork for collecting scats was conducted in 2018 and 2019, in the same or similar manner across all three countries. The teams designed fixed transects and frequently visited the study area, covering the transects either by foot or by car, wherever possible. All scats detected along the routes were collected. A total of 51 transects were defined: 25 in North Macedonia, 16 in Albania and 10 in Greece (Figure 1). They were surveyed at more or less frequent intervals: North Macedonia every 7–10 days, Greece once per month and Albania at least three 4–5-day field outings per season. Every opportunistic find outside those transects was also collected (especially in Greece, where the majority of analysed scats were found opportunistically). The habitat of each scat was defined according to an internally defined classification, which was loosely based on the EUNIS level 2 classification (Moss 2008). The collecting period was split into seasons, spring (15 Mart–14 June), summer (15 June–14 September) and autumn (15 September–14 December), with a target set to 30 scats per country for each season, except for the autumn period, where the target was increased to 70 samples per country. In Greece, an additional focus of this particular study was the analysis of scats found in the agricultural zone, where increasing human-bear conflict has been seen in recent years. Therefore, the target sample size was increased by additional 30 samples in summer and autumn each, for the agricultural zone in Greece.

All scats found in the field were collected in big ziplock bags with a standardized form used in all three countries. Each scat was assigned a unique ID and a database was created in the smartphone app Memento Database (v. 4.10) to keep track of all important information. After the field, all collected samples were kept frozen until enough samples were collected for laboratory analysis.

### *Laboratory analysis*

The laboratory analysis was carried out in two phases. In the first phase, all scats were measured for their mass and total volume, using a digital scale for the former and graduated cylinders for the latter. In the second phase, the scats were washed through a sieve, and the species of all items remaining in the sieve were identified to the lowest taxonomic level possible.

The volume of each food item in a scat was measured by water displacement to the nearest millilitre, giving the percent volume of each identified item (Cicnjak et al. 1987). The difference between the sum of volumes of all identified items and the total scat volume was labelled as unidentified. In most cases, that referred to the amorphous mass that was almost or fully digested.

### *Data analysis*

The frequency of occurrence (F%) for each food item was calculated by dividing the number of times that item was present in the scats (*n*) by the total number of all scats (*N*), expressed in percentage:

$$\boldsymbol{F\%} = \frac{\boldsymbol{n}}{\boldsymbol{N}} \cdot \mathbf{100}$$

Similarly, the percent volume (V%) of each item was calculated as a percent of the total volume. The frequency of occurrence approach has a tendency to underestimate the importance of the dominant food items. Thus, we calculated the importance value percentage (IV%) for each food item by dividing the product of their F% and V% by 100.

To measure diet specialisation, trophic niche breadth was calculated for the total diet, for each season, and for each country. For this, we used Levin's index for niche breadth:

$$\boldsymbol{B} = \frac{\mathbf{1}}{\sum \boldsymbol{p_j^2}},$$

where $p_j$ is the proportion of food item *j* in the total diet (Levins 1968). The value of the Levin's index was then standardised on a scale from 0 to 1 (0 being an extreme specialist, and 1 being a generalist with equal use of all food items) using the following equation (Krebs 1999):

$$\boldsymbol{B_{st}} = \frac{\boldsymbol{B-1}}{\boldsymbol{N-1}},$$

where N represents the total number of food items. For the same categories, we also calculated trophic diversity using the Shennon-Wiener index *H'* (Colwell and Futuyma 1971) and standardised it on a 0-1 scale with the Pielou's Evenness measure *J'* (Pielou 1977).

Finally, to assess the similarity of the diet between countries, we calculated the Morisita-Horn index for niche overlap ($C_{MH}$, Horn 1966), Pianka's measure of overlap (Krebs 1999) and the Bray-Curtis dissimilarities index for each country pair (Bray and Curtis 1957; Ofori et al. 2023). Because of the highly concordant results between the three, and because most related papers use it, we will only present and discuss the Morisita-Horn index.

In order not to underrepresent the highly digestible food items, such as meat and acorns, and overestimate the poorly digestible ones, like grasses, we used conversion factors (CF), introduced by Hewitt & Robbins (1996), and further developed in subsequent studies (Dahle et al. 1998; Bojarska and Selva 2013; López-Alfaro et al. 2015). The percent volume (V%) of each food item is multiplied by its corresponding CF to yield the estimated dietary content (EDC). We used the following correction factors: 0.24 for grasses, 0.59 for wheat and 1.18 for maize, from 1.18 to 1.5 for the different hard masts (acorns, beech nuts and hazelnuts), from 0.51 to 1.93 for the different soft masts (all fruits), 3 for ungulates and other large mammals and 4 for small mammals and reptiles. All statistical analyses were conducted using MS Excel.

Ant and grass species were identified at the taxonomic level of family. The ants were always found mixed with soil, so their volume could not be accurately measured. In those cases, we agreed to have a uniform way of quantifying it and stated the ant volume to be 0.5 ml. All fruits were identified to the taxonomic level of species or, in a few cases, to genus. In cases where small amounts of seeds were found, we stated 1 ml for each wild cherry and European cornel seed and 1.5 ml for each cherry plum seed. For apples and wild pears, the volume of seeds was stated as 0.5 ml per seed. All macroscopically undetermined seeds and hairs were identified using an optical microscope and dichotomous identification keys (Hausman 1920; De Marinis and Agnelli 1993; Teerink 2003; De Marinis and Asprea 2006; Felix et al. 2014; Cornally et al. 2016). Examination of the hair medulla was done using synthetic resin, and for the hair cuticle, a clear nail polish was used as a medium for imprinting the outermost structure of the hair shaft.

To estimate the bear diet by season, we calculated the "true date" by adjusting the date of collection with the visually estimated age of the scat. Each "Age of scat" category was approximated using its median value, indicating the number of days to be subtracted from the date of collecting. The assigned number of days for each category is as follows: 0–1 day = 0; 2–5 days = 3; 6–15 days = 10; 16–30 days = 23; 1–3 months = 61; 3-6 months = 137; older than 6 months = 200.

With the new dates, the samples were split into three seasons: spring from 1 March to 31 May, summer from 1 June to 31 August, and autumn from 1 September to 30 November. These seasons were selected despite the different dates used in the collecting period mentioned above, in order to provide more comparable results with other studies. Samples that were up to four days out of the seasons, were classified as being part of the nearest season (spring or autumn). Three samples were considerably out of the three seasons and were discarded from the diet analysis.

## Results

A total of 550 scats were analysed from all three sides of Prespa (Figure 1). Of those, 117 were collected from the Albanian side of Prespa, 125 from the Macedonian side, and 308 from the Greek side.

From the total number of scats, 87 were 0–1 day old, 206 were 2–5 days old, 125 were 6–15 days old, 101 were 16–30 days old, 26 were 1–3 months old, four were 3–6 months old and one was older than 6 months. When taking these values into account, the true dates show 57, 181 and 315 samples from spring, summer, and autumn, respectively.

The average scat volume was 418.1 ml (range 10–2880 ml) and the average scat mass was estimated to be 447 g (range 10–2843 g).

The scats were collected from 22 different habitats, giving insight into the habitat preference by the brown bear. The most preferred habitats were oak forests, mixed forests, agricultural lands with natural areas and abandoned agricultural lands (Figure 2).

The most prominent food source for the bears was cherry plums (*Prunus cerasifera*), which were identified in 263 scat samples, with a frequency of occurrence of 47.82% (Table 1). This food item also had the highest importance value for the diet, with IV% = 9.56% (Table 1). The cherry plums were the most frequent item in all three countries (Table 1). While in both Albania and

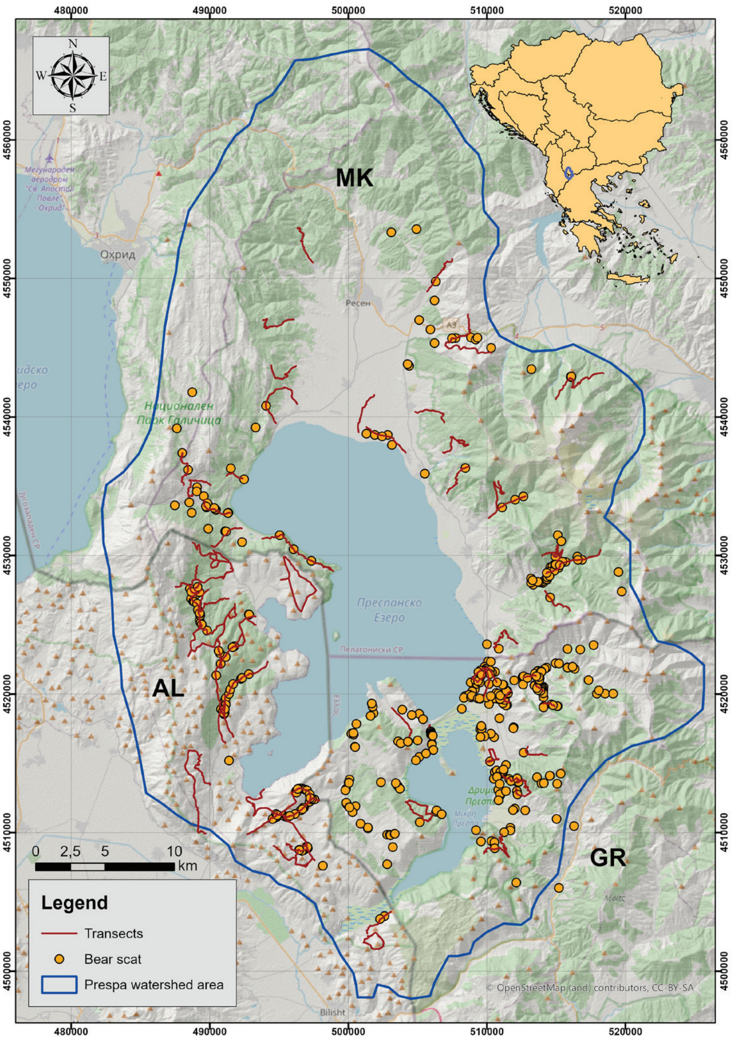


**Figure 1**. Map of all the transects and collected samples from the transboundary Prespa basin

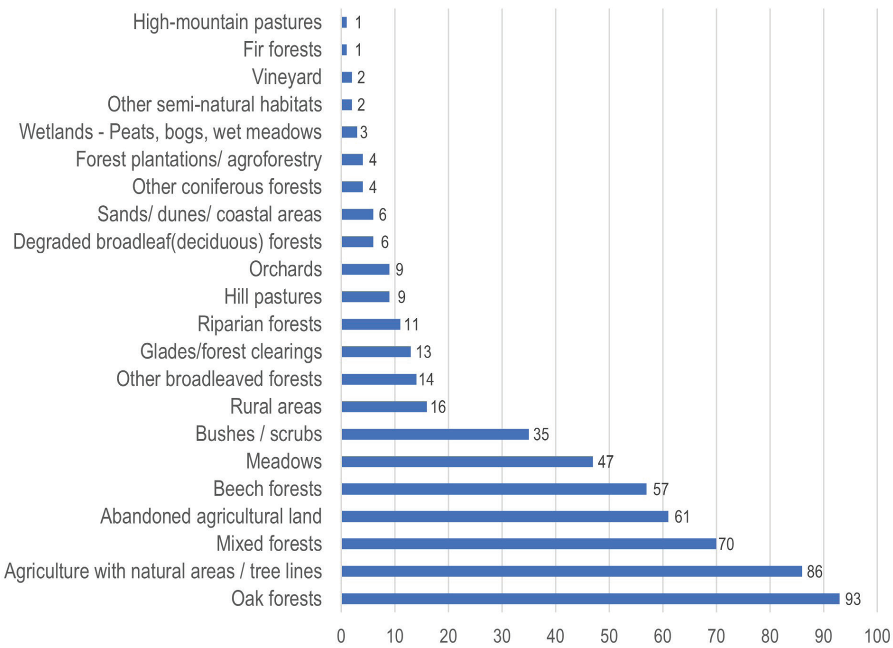


**Figure 2**. Number of samples found in different habitats.

Greece, the cherry plums had also the highest IV% value (14.25% and 11.06% respectively), in North Macedonia apples were by far the most important food source for the bears, with IV% = 20.53% (Table 1). In Albania, the acorns were a frequent choice for bears (F% = 28.21%), and in the agricultural zone in Greece, wild pears were preferred by the bears found in nearly a third of the samples (F%= 29.3%).

Compared to the plant-based portion of the brown bear diet, its carnivorous dietary habit was significantly less prominent. The most notable food items in this category are ants (Formicidae), found in 38 scat samples, Hermann's tortoise (*Testudo hermanni*) found in 18 samples, and wild boar (*Sus scrofa*) found in 11 samples (Table 1). Other traces of food of mammal origin were found in the form of hair, crushed bones, or skin. In total, 26 scats contained mammal remains, of which only 8 were detected as coming from livestock (goat and sheep). It is important to note that all mammal food sources had an importance value of less than 0.01% (Table 1).

Finally, 203 scats had some parts from the total volume that were fully digested and were treated as unidentified.

In spring, the largest portion of the scats in Greece contained grasses (*Poaceae*). In Albania, besides the grasses, ants and acorns were also very common. In North Macedonia, however, most scats contained apples as the most prevalent food item (Table 2). In summer, in all three countries cherry plums are the predominant food item, especially in Albania, where it was found in over 80% of the collected samples (Table 2). In autumn, the cherry plums were predominant yet again, although a noticeable increase in acorn intake is present in all countries. But in North Macedonia, the autumn diet is largely shifted towards apples (Table 2).

The use of correction factors changes the proportions of many items. The cherry plums are again the most important food source, with EDC = 38.6%. The value for apples drops to only 8.82%, while the EDC of acorns is increased to 20.53% (Table S1). The estimated dietary content of ungulates, even though increased by the correction factor, is still under 1%, meaning that ungulates play a minor role in the diet of Prespa bears.

The breadth of the trophic niche for the total diet was $B_{st}$ = 0.26 (B = 7.44), suggesting a propensity toward specialisation. In terms of seasons, the bears had the most generalist diet in spring, where we computed $B_{st}$ = 0.48 (B = 7.74), and the most specialised diet in summer, with $B_{st}$ = 0.19 (B = 4.68). In autumn, Levin's index was $B_{st}$ = 0.26 (B = 6.95). Albania boasts the broadest niche, with $B_{st}$ = 0.37 (B = 6.98), while Greece features the narrowest ($B_{st}$ = 0.28, B = 6.97). In North Macedonia we calculated $B_{st}$ = 0.3 (B = 5.93).

Regarding the trophic diversity of the total diet, the Shannon index and the Pielou evenness index were estimated to be H' = 2.4 and J' = 0.74. The diversity was lowest in summer (H' = 1.95, J' = 0.65), while the values were more similar in spring and autumn (H' = 2.28, J' = 0.84 and H' = 2.3, J' = 0.72, respectively). The trophic diversity was quite uniform across the countries: Albania (H' = 2.3, J' = 0.81), North Macedonia (H' = 2.11, J' = 0.74) and Greece (H' = 0.23, J' = 0.74).

The Morisita-Horn index between the countries points to a considerable overlap in the dietary niche: $C_{MH}$ = 0.84, for North Macedonia-Greece, $C_{MH}$ = 0.87

**Table 1**. Count (N) and frequency of occurrence (F%) of each identified food item, total and by country. Values for the agriculture area in Greece are presented in parentheses.

| | Total | | | Albania | | | N. Macedonia | | | Greece | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | IV% | F% | V% | IV% | F% | V% | IV% | F% | V% | IV% | F% | V% |
| **Plants** | | | | | | | | | | | | |
| **Hard masts** | | | | | | | | | | | | |
| *Quercus* sp. | 2.51 | 18.36 | 13.69 | 6.91 | 28.21 | 24.50 | 0.70 | 12.1 | 5.81 | 2.56 | 17.15 (12.12) | 14.92 |
| *Fagus sylvatica* | 0.02 | 2.36 | 1.04 | 0.14 | 4.27 | 3.29 | <0.01 | 2.42 | 0.07 | 0.02 | 1.62 | 0.96 |
| *Corylus avellana* | <0.01 | 1.09 | 0.22 | 0.08 | 5 | 1.56 | | | | | | |
| **Soft masts** | | | | | | | | | | | | |
| *Prunus cerasifera* | 9.56 | 47.82 | 20.00 | 14.25 | 45.30 | 31.46 | 4.62 | 41.94 | 11.02 | 11.06 | 51.13 (50.51) | 21.63 |
| *Malus domestica* | 2.70 | 15.64 | 17.30 | 0.02 | 2.6 | 0.68 | 20.53 | 40.32 | 50.92 | 0.51 | 10.68 (18.18) | 4.80 |
| *Prunus avium* | 1.24 | 15.27 | 8.10 | <0.01 | 0.85 | 0.02 | 0.47 | 15.32 | 3.05 | 2.60 | 20.71 (5.05) | 12.56 |
| *Cornus mas* | 0.55 | 11.64 | 4.69 | 1.23 | 13.68 | 8.98 | 0.16 | 6.45 | 2.45 | 0.62 | 12.94 (22.22) | 4.75 |
| *Pyrus pyraster* | 0.24 | 9.5 | 2.58 | 0.03 | 5 | 0.55 | | | | 0.65 | 14.89 (29.29) | 4.34 |
| *Rubus* spp. | 0.03 | 3.27 | 0.77 | <0.01 | 1.71 | <0.01 | 0.05 | 4.84 | 1.00 | 0.03 | 3.24 (5.05) | 0.84 |
| *Juglans regia* | 0.02 | 2.55 | 0.86 | | | | | | | 0.07 | 4.53 (6.06) | 1.50 |
| *Vitis vinifera* | <0.01 | 1.82 | 0.28 | 0.06 | 3.42 | 1.66 | <0.01 | 0.81 | 0.05 | <0.01 | 1.62 (4.04) | 0.05 |
| *Rosa canina* | 0.02 | 1.64 | 1.22 | 0.13 | 3.42 | 3.69 | 0.05 | 2.42 | 2.11 | <0.01 | 0.65 (2.02) | 0.18 |
| *Ficus carica* | <0.01 | 0.36 | 0.23 | | | | | | | <0.01 | 0.65 | 0.41 |
| *Zea mays* | <0.01 | 0.36 | <0.01 | <0.01 | 0.85 | 0.01 | | | | <0.01 | 0.32 | <0.01 |
| *Crataegus monogyna* | <0.01 | 0.18 | 0.02 | | | | <0.01 | 0.81 | 0.08 | | | |
| *Juniperus communis* | <0.01 | 0.18 | 0.25 | | | | <0.01 | 0.81 | 0.87 | | | |
| **Other plant material** | | | | | | | | | | | | |
| *Triticum vulgare* | <0.01 | 1.64 | 0.20 | 0.11 | 7.7 | 1.44 | | | | | | |
| *Poaceae* | 1.72 | 20.00 | 8.58 | 0.52 | 12.0 | 4.33 | 1.48 | 19.35 | 7.65 | 2.35 | 23.3 (24.24) | 10.08 |
| **Animals** | | | | | | | | | | | | |
| **Insects** | | | | | | | | | | | | |
| *Formicidae* | <0.01 | 7.09 | <0.01 | <0.01 | 14.53 | 0.03 | <0.01 | 4.03 | <0.01 | <0.01 | 5.5 (7.07) | <0.01 |
| **Reptiles** | | | | | | | | | | | | |
| *Testudo hermanni* | <0.01 | 3.27 | 0.19 | 0.05 | 7.7 | 0.61 | 0.01 | 4.03 | 0.34 | <0.01 | 1.29 (2.02) | 0.02 |
| **Mammals** | | | | | | | | | | | | |
| *Sus scrofa* | <0.01 | 2.00 | <0.01 | <0.01 | 2.6 | <0.01 | <0.01 | 1.61 | <0.01 | <0.01 | 1.94 (1.01) | <0.01 |
| *Ovis aries* | <0.01 | 0.9 | 0.11 | | | | <0.01 | 0.81 | 0.28 | <0.01 | 1.29 (2.02) | 0.05 |
| *Canis lupus familiaris* | <0.01 | 0.73 | <0.01 | | | | <0.01 | 0.81 | <0.01 | <0.01 | 0.97 (1.01) | <0.01 |
| *Capra aegagrus hircus* | <0.01 | 0.55 | 0.19 | | | | | | | <0.01 | 0.97 (1.01) | 0.33 |
| *Capreolus capreolus* | <0.01 | 0.36 | <0.01 | | | | | | | <0.01 | 0.65 | <0.01 |
| *Lepus europaeus* | <0.01 | 0.18 | <0.01 | | | | | | | <0.01 | 0.32 (1.01) | <0.01 |

for Greece-Albania and $C_{MH}$ = 0.71 for Albania-North Macedonia.

## Discussion

This study yields the first fully comprehensive insight into the brown bear dietary habits in the Prespa basin. The results show that the diet, and possibly even the behaviour, of the brown bear differ to some degree in all three countries. The largest difference in the diet is evident between Albania and North Macedonia, as indicated by the niche overlap analysis ($C_{MH}$ = 0.71). Autumn was the most productive season in terms of finding scats. Even though this is partially explained by our increased efforts, the more important conclusion is that the feeding activities of bears are increased (hyperphagia) in the pre-hibernation period (Ruiz-Villar et al. 2019).

Generally, the feeding habits of the bears are more or less in tune with the seasonal availability, following the plants' phenological cycles (Bowersock et al. 2023).

**Table 2**. Frequencies of occurrence (F%) by country and season

| Food item | Albania | | | North Macedonia | | | Greece | | |
|---|---|---|---|---|---|---|---|---|---|
| | spring | summer | autumn | spring | summer | autumn | spring | summer | autumn |
| **Plants** | | | | | | | | | |
| **Hard masts** | | | | | | | | | |
| *Quercus* sp. | 28.57 | | 36.49 | 11.11 | | 14.29 | 29.41 | | 29.63 |
| *Fagus sylvatica* | 4.76 | | 5.41 | | | 3.90 | 5.88 | | 2.47 |
| *Corylus avellana* | 4.76 | 4.55 | 5.41 | | | | | | |
| **Soft masts** | | | | | | | | | |
| *Prunus cerasifera* | 9.52 | 81.82 | 44.59 | 5.56 | 40 | 40.26 | 11.76 | 58.91 | 49.38 |
| *Malus domestica* | 9.52 | | 1.35 | 44.44 | 6.67 | 48.05 | | 3.10 | 17.90 |
| *Prunus avium* | | 4.55 | | 5.56 | 46.67 | 5.19 | 5.88 | 47.29 | |
| *Cornus mas* | | 18.18 | 16.22 | 5.56 | | 9.09 | | 5.43 | 20.37 |
| *Pyrus pyraster* | 4.76 | | 6.76 | | | | | 8.53 | 21.60 |
| *Rubus* spp. | 4.76 | | 1.35 | | | 6.49 | | 3.10 | 3.70 |
| *Juglans regia* | | | | | | | | 0.78 | 8.02 |
| *Vitis vinifera* | | 9.09 | 2.70 | | | 1.30 | | | 3.09 |
| *Rosa canina* | | 4.55 | 4.05 | 11.11 | 3.33 | | | | 1.23 |
| *Ficus carica* | | | | | | | | | 1.23 |
| *Crataegus monogyna* | | | | | 3.33 | | | | |
| *Juniperus communis* | | | | | | 1.30 | | | |
| **Other plant material** | | | | | | | | | |
| *Triticum vulgare* | 19.05 | 9.09 | 4.05 | | | | | | |
| *Zea mays* | | | 1.35 | | | | | 0.78 | |
| *Poaceae* | 23.81 | 4.55 | 10.81 | 22.22 | 20 | 12.99 | 47.06 | 26.36 | 18.52 |
| **Animals** | | | | | | | | | |
| **Insects** | | | | | | | | | |
| *Formicidae* | 33.33 | 31.82 | 4.05 | | 13.33 | 1.30 | 11.76 | 10.08 | 1.23 |
| **Reptiles** | | | | | | | | | |
| *Testudo hermanni* | 14.29 | 4.55 | 6.76 | 22.22 | | 1.30 | | 2.33 | 0.62 |
| **Mammals** | | | | | | | | | |
| *Sus scrofa* | | | 1.35 | | 6.67 | | | 0.78 | 3.09 |
| *Ovis aries* | | | | | | | | 1.55 | 1.23 |
| *Canis lupus familiaris* | | | | | | 1.30 | 5.88 | 0.78 | 0.62 |
| *Capra aegagrus hircus* | | | | | | | | 2.33 | |
| *Capreolus capreolus* | | | | | | | | | 1.23 |
| *Lepus europaeus* | | | | | | | | | 0.62 |

In spring, the frequencies of occurrence of fruits were notably lower compared to the other seasons. The food niche was widest in this season, indicating that the bears opted for a more generalist diet ($B_{st}$ = 0.48), which is usually the case when the abundance of food is lower (Evans et al. 2005; Lesser et al. 2020). The most frequent items were grasses, acorns and ants. The only outlier were the apples in North Macedonia, found in over 40% of the spring scats. This can be explained by the massive apple plantations in the region, given that 2018 was an exceptionally fruitful year for apples. Heaps of unsold apples ended up disposed in landfills, thus ensuring food for the bears even in early spring the following year. Besides this, it is noteworthy that no specific artificial feeding stations for wildlife are present in the researched area. In summer, the peak occurrence of fruits like wild cherries and cherry plums is evident, which ripen in early summer and mid-to-late summer, respectively. This is further confirmed by the narrowest food niche breadth ($B_{st}$ = 0.19), alluding to a more specialised diet. Following the end of summer, the trophic niche is broadening again ($B_{st}$ = 0.26). This is the time when wild cherries are becoming less dominant and are being replaced with seasonally available apples and wild pears, as well as cornelian cherries. Acorns are preferred by the bears in autumn, providing a fatty mast that is nutritional and energy-packed for the winter months (López-Alfaro et al. 2013, 2015).

The third most common food source in Albania throughout the entire study period were ants, found in one-third of scats from both spring and summer. This could potentially indicate that there was fruit scarcity, as it wasn't the case in the other countries, where the largely available wild cherries were preferred by bears. One other noteworthy item in Albania was wheat (*Triticum vulgare*). This food source was present in 9 samples exclusively in this part of the region and in all three seasons. In spring this source was detected in over 19% of the samples. To support this claim further, the bears in Albanian Prespa had the most generalist diet ($B_{st}$ = 0.37) from all three countries.

The spectrum of food items that are selected by the bears in Prespa seems to be largely unchanged since the last estimate conducted by Mertzanis et al. (2000), although the proportion (and, likely, the importance) of the individual food items has shifted in the past two decades. While fruits from the genus *Prunus* are still one of the paramount food choices for the bears (F% = 44.8% in the 1990s and F% = 47.8% for *P. cerasifera* in our study), the occurrence of beech nuts has notably decreased (from being the dominant food item with F% = 48.9% in the 1990s, they were present in only 2.4% in our samples). A few hypotheses can be put forward to explain this. Firstly, it could be related to the timing of the studies, potentially coinciding with high and low yield beech nut years. Secondly, this might allude to an increased boldness of the bears to venture into orchards and lowlands. Alternatively, this change could be associated with the region's substantial human depopulation over the last several decades, with a noticeable increase in emigration as evidenced by local census data.

A few potential weaknesses were identified during the study. Among these is the recurring problem of facing difficulties finding samples in all the countries. The only country that managed to achieve the set target was Greece in summer 2018 in the non-agricultural zone (74) and also in autumn 2018 and summer 2019, combining both the agricultural and non-agricultural zones (72 and 53 respectively). The least successful season was spring when the target was not achieved in any country in both years and the least successful season per country was the summer of 2019 in North Macedonia with only one collected scat. One possible factor for this issue was that acorns were at their cyclic high season in the summer of 2019 and especially in 2018. This could prevent the bears from descending lower into the settlements in search of food, to avoid potential conflict with humans or stray dogs. That in turn prevented the teams from successfully locating the scats in the dense oak forests. Another possible weakness of the study was that the different moisture (or lack thereof) of the scats meant that they would respond differently to the water used for measuring the volume in the graduated cylinders. Some older scats that contained drier items, like grasses, absorbed a portion of the water and that could temper with the final volume measurements. To increase the accuracy of this analysis for future studies, we recommend using scats which are not older than 15 days for spring and autumn samples, and 7 days for samples collected during the summer. The overall weakness of field identification scat-analysis studies has been previously discussed in multiple papers (Klare et al. 2011; Morin et al. 2016). Nevertheless, it still remains a relatively inexpensive method which gives a decent insight and provides a good basis for comparison between different populations. A future study on the diet of the Prespa bears could consider applying more state-of-the-art approaches, such as DNA barcoding (De Barba et al. 2014).

It is a generally safe assumption that the brown bear diet in the Prespa region is mainly plant-based, especially when fruits are in season (as demonstrated in many other studies, e.g. Cicnjak et al. 1987; Clevenger et al. 1992; Naves et al. 2006; Paralikidis et al. 2010). It is not uncommon for bears to cause damage to crops and orchards and in a few cases during the study period, we found evidence for it. The presence of wheat in the scats from Albania could also support this. Concerning the carnivorous aspect of their diet, with our method we were able to detect remains of domestic ungulates in only eight scat samples and in small volumes. Using correction factors somewhat improves the estimate and reduces underestimation, but it still needs to be interpreted with caution. Perhaps using a protein-based analysis could yield a deeper insight into the carnivorous part of the Prespa bear diet. Regardless, there were no reported cases of active predation on livestock in the area, meaning that the ungulates detected in the scat samples likely came from scavenging on carrion. The bear's kleptoparasitism on the prey of other large carnivores has been known from previous and unrelated studies (Krofel et al. 2012; Ordiz et al. 2015; Allen et al. 2021). However, active predation of the bears on tortoises has previously been confirmed in the Balkans (Krofel 2012), and their detection in our samples from all three countries could point to an alternative and important source of protein.

Given the heterogeneous landscape and different anthropogenic pressures in the three countries, it is important to keep these results in mind when proposing conservation measures for the brown bear. A recent genetic study (Skrbinšek et al. 2021) has concluded that the genetic diversity of bears in Prespa is lower compared to the other subpopulations in the Dinaric-Pindos population (Linnell et al. 2008), and that there are considerable gene flow limitations (Tsalazidou-Founta et al. 2022), thus solidifying the importance of improving habitat connectivity. Furthermore, a telemetry study on bears in Prespa will complement the dietary habits of the species by revealing the corridors they use to traverse between the three countries (Hoxha et al. in prep).

The results of this study could be implemented in future conservation and management action plans, ensuring a more sustainable development of the region, especially in the light of the vastly different agricultural and forest management practices. These kinds of analyses can be a valuable asset in areas where the populations of this large carnivore are larger, to lessen the potential human-bear conflict (Treves et al. 2006).

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**Author contributions:** All authors participated in the field collection of scats. AG, AP, OL, OA, JH, DM and IS contributed to the lab analyses. AG conducted the data analysis and wrote the draft manuscript. All authors gave editorial comments and contributed to completing the final manuscript. AP performed the proofreading of the manuscript and translated the abstract to Macedonian.

All authors of this paper declare that they have no conflicts of interest.

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## Supplementary material

**Table S1**. Percent volume (V%) of each detected item, along with the Estimated Dietary Content (EDC), obtained with the use of correction factors (CF), total and by season.

| | Total | | Spring | | Summer | | Autumn | |
|---|---|---|---|---|---|---|---|---|
| Food item | V% | EDC | V% | EDC | V% | EDC | V% | EDC |
| **Hard masts** | | | | | | | | |
| Quercus sp. | 13.69 | 20.53 | 18.79 | 28.18 | | | 20.07 | 30.1 |
| Fagus sylvatica | 1.04 | 1.22 | 4.17 | 4.93 | | | 1.09 | 1.29 |
| Corylus avellana | 0.22 | 0.35 | 0.004 | 0.01 | 0.07 | 0.1 | 0.35 | 0.55 |
| **Soft masts** | | | | | | | | |
| Prunus cerasifera | 20 | 38.6 | 0.28 | 0.53 | 24.33 | 46.95 | 20.49 | 39.54 |
| Malus domestica | 17.3 | 8.82 | 42.45 | 21.65 | 0.43 | 0.22 | 20.25 | 10.33 |
| Prunus avium | 8.1 | 15.63 | 1.08 | 2.08 | 24.94 | 48.13 | 0.64 | 1.23 |
| Cornus mas | 4.69 | 9.06 | 0.01 | 0.01 | 0.63 | 1.21 | 7.91 | 15.27 |
| Pyrus pyraster | 2.58 | 3.09 | 0.01 | 0.01 | 2.51 | 3.01 | 3.23 | 3.87 |
| Rubus spp. | 0.77 | 0.67 | 0.004 | 0.00 | 0.3 | 0.26 | 1.19 | 1.04 |
| Juglans regia | 0.86 | 1.29 | | | 0.01 | 0.02 | 1.51 | 2.26 |
| Vitis vinifera | 0.28 | 0.34 | | | 0.31 | 0.37 | 0.33 | 0.4 |
| Rosa canina | 1.22 | 1.47 | 3.63 | 4.35 | 0.82 | 0.98 | 1.09 | 1.31 |
| Ficus carica | 0.23 | 0.28 | | | | | 0.41 | 0.49 |
| Crataegus monogyna | 0.02 | 0.03 | | | 0.07 | 0.09 | | |
| Juniperus communis | 0.25 | 0.13 | | | | | 0.43 | 0.23 |
| **Other plant material** | | | | | | | | |
| Triticum vulgare | 0.2 | 0.12 | 0.55 | 0.33 | 0.5 | 0.29 | 0.004 | 0.002 |
| Zea mays | 0.002 | 0.002 | | | 0.001 | 0.001 | 0.003 | 0.003 |
| Poaceae | 8.58 | 2.06 | 11.7 | 2.81 | 12.19 | 2.93 | 6.37 | 1.53 |
| **Insects** | | | | | | | | |
| Formicidae | 0.01 | 0.01 | 0.02 | 0.02 | 0.01 | 0.01 | 0.002 | 0.003 |
| **Reptiles** | | | | | | | | |
| Testudo hermanni | 0.19 | 0.76 | 0.9 | 3.60 | 0.04 | 0.17 | 0.16 | 0.63 |
| **Mammals** | | | | | | | | |
| Ungulates | 0.3 | 0.9 | | | 0.74 | 2.22 | 0.004 | 0.01 |
| Lepus europaeus | 0.0002 | 0.001 | | | | | 0.0004 | 0.002 |
| Canis lupus familiaris | 0.002 | 0.01 | 0.002 | 0.01 | 0.001 | 0.002 | 0.001 | 0.002 |