



Research Article

Ants in brown bear diet, and discovery of a new ant species for Estonia from brown bear scats

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Abstract

For omnivorous brown bears, ants can seasonally constitute an important category of food with high nutritional value. A former dietary study conducted in Estonia revealed that the energy gained from animal and plant food was roughly equal, whereas the contribution of ants was almost 15%. Here, using the same dataset, we analyzed ant consumption by brown bears in Estonia at a greater taxonomic resolution and evaluated the preferences of brown bears towards different ant species by measuring the availability (biomass and mound density) of ants in the study area. Among the 18 species and five groups of ants in bear scats, members of the genera *Lasius* and *Formica* were the most abundantly consumed ant groups, considering both the volume and frequency of occurrence. Among the species we detected, *Lasius niger* and *Formica polyctena* dominated. However, these were not the favorite ant taxa for bears, that highly preferred *Camponotus* ants and avoided *Myrmica* ants. In addition, a new species (*Camponotus fallax*) for Estonian ant fauna was discovered, providing an example of how studies on mammal food habits can reveal elusive insect species that have remained undiscovered with traditional survey methods. The general pattern of the brown bear myrmecophagy in Europe is examined to place our results into a broader context.

Introduction

The brown bear (*Ursus arctos*) is an opportunistic omnivore consuming wide variety of food items throughout its geographical range (e.g. Vulla et al., 2009; Bojarska and Selva, 2012; Ciucci et al., 2014; Gunther et al., 2014; Stenset et al., 2016). Despite the relatively large differences in dietary habits between geographically distant bear populations, studies have indicated that in most populations bears consume ants (Formicidae), often as a dominating family-group among insects (e.g. Pažetnov, 1990; Mattson et al., 1991; Swenson et al., 1999; Große et al., 2003; Tosoni et al., 2018). Ants may seasonally constitute approximately one third of the estimated dietary energy content in some European brown bear populations (Ciucci et al., 2014; Stenset et al., 2016). Dietary data collected in the Great Yellowstone Ecosystem during almost four decades have revealed that ants were among the most frequently and consistently used food items (Gunther et al., 2014), despite the fact that ants have been considered energetically not so important for grizzly bears (Mattson, 2001).

The selection of food depends not only on its availability and abundance, but also on energetic and nutritional requirements of animals. Myrmecophagy — the consumption of ants — results from their high abundance, making ants a stable food source rich in protein, fat and energy (Johansen, 1997; Mattson, 2001; Große et al., 2003; Coogan et al., 2014; Pekár and Mayntz, 2014) and providing essential amino acids (Yamazaki et al., 2012). While the factors behind consumption

of ants by bears in different regions are not fully understood, it is often proposed that ants are a secondary food resource, primarily used when other protein-rich foods (e.g. mammals, salmon) are less available (Swenson et al., 1999; Mattson, 2001; Gunther et al., 2014). However, the studies in Slovenia and Sweden have demonstrated that even if there are large discrepancies in the available biomass of ants for brown bears in different regions ants can still be consumed at comparable level (Swenson et al., 1999; Große et al., 2003). These results indicate that at least in some regions ants may be actually more than just secondary food resource (Große et al., 2003). Variations in degree of ant consumption are related to sex and reproductive status of bears. In general, females tend to consume more ants compared to males (Johansen, 1997; Elgmork and Unander, 1999). Moreover, females with cubs, as well as subadult females, tend to consume significantly more ants compared to females without cubs, as indicated in black bears (*Ursus americanus*; Bull et al., 2001). This can be explained at least partly by the differences of nutritional requirements Hildebrand et al., 1999; López-Alfaro et al., 2013. Additionally, the study on Yellowstone grizzly bears (Mattson, 2000) has suggested that consumption of ants has impact on cub survival, as females eating more ants were more successful in keeping their cubs alive.

Brown bear myrmecophagy has been studied extensively in Scandinavia (Elgmork and Kaasa, 1992; Johansen, 1997; Elgmork and Unander, 1999; Swenson et al., 1999), but also in Slovenia (Große et al., 2003), Italy (Tosoni et al., 2018) and in the Yellowstone ecosystem in North-America (Mattson, 2001). In these studies ants were often identified below the family level (usually to the level of genus or species group). Moreover, ant selection and preferences by bears were analyzed

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by including ant availability data and/or by analyzing bear foraging behavior in the field. Additionally, myrmecophagy has been examined in American black bears (Noyce et al., 1997; Auger et al., 2004) and Asiatic black bears (*Ursus thibetanus*; Yamazaki et al., 2012; Fujiwara et al., 2013).

The brown bear population in Estonia is distributed all over the mainland (Valdmann et al., 2001) and, according to official data (based on information gathered from hunters), the approximate population size has been 500–700 individuals for years, with a hunting bag between 5–8% of the total population size. The Estonian bears belong to a large clade of Holarctic brown bears and have maintained the gene flow, albeit limited, with the neighbouring populations of Latvia and Russia (Saarma et al., 2007; Korsten et al., 2009; Tammeleht et al., 2010; Keis et al., 2013; Anijalg et al., 2018). Previous brown bear dietary analysis in Estonia has revealed that ants were the most frequently eaten invertebrates (Vulla et al., 2009). However, the importance of different ant genera and species, as well as bear preferences, were not investigated. Different ant taxa differ in nutritional content (Noyce et al., 1997; Swenson et al., 1999; Auger et al., 2004) and knowledge about the consumption of different ant species can provide valuable insights into bear feeding ecology. The aims of this study were to: (1) estimate seasonal variation in the consumption of different ant taxa among bears in Estonia, (2) determine ant availabilities and preferences by brown bears, and (3) review myrmecophagy in European bear populations and discuss within a European context.

Materials and Methods

The study area

The study was performed in three counties of north-eastern Estonia: Jõgevamaa, Lääne-Virumaa and Ida-Virumaa (Fig. 1) during 2003–2004. The area is approx. 9400 km² (1/5 of Estonia) and it is a core area for the brown bear population (Valdmann et al., 2001), comprising 55% of approximately 550 bears of the country during the study period (Statistics Estonia). In this area the coniferous Euro-Siberian taiga transitions into a European zone of deciduous forests. Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), silver birch (*Betula pendula*) and aspen (*Populus tremula*) are the dominant tree species. Approximately 43% of Lääne-Virumaa, 56% of Jõgevamaa and 65% of Ida-Virumaa were covered by forest. The average temperature is 6.1 °C and vegetation period lasts for 120–130 days, from late April to September. About 600 mm of precipitation fall during a year and snow cover usually lasts for 4 months (December–March). The brown bear was managed as a game animal in Estonia until 2004 and was hunted under a quota system. Since 2004, when Estonia joined European Union (EU), Estonia has complied with EU regulation that bear hunting should be allowed only to mitigate bear-human conflicts. Based on energetic contribution, the most important food items for Estonian bears are cereals, mammals, fruits/berries and ants, listed in a decreasing order (Vulla et al., 2009). Potential prey species for bears are moose (*Alces alces*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*). Additionally, carcasses of livestock, potatoes, apples and grain were available at the feeding sites.

Scat analysis

Crew of the project and local hunters collected opportunistically 142 bear scats during all field activities from brown bears core range during 2003–2004 for the bear dietary study (Vulla et al., 2009). Scats were collected into plastic bags, labelled and frozen at –20 °C until further analyses. To analyse seasonal differences in food consumption, the year was divided into three seasons based on availability of major food items as described in Dahle et al. (1998): spring (April–last third of May), summer (last third of May–July) and autumn (August–October).

Analysis of dietary items in scat content was performed by Vulla et al. (2009) and references therein. Ants in each analyzed subsample were stored for species identification. Ant abundance was described in term of faecal volume (FV) and frequency of occurrence (FO) (Johansen, 1997; Dahle et al., 1998). FV is defined as the average percent



Figure 1—Map of Estonia where different counties are border lined and location of Estonia in Europe shown in inset figure. The study area is striped and comprises three counties: 1: Lääne-Virumaa; 2: Ida-Virumaa; 3: Jõgevamaa.

volume of each taxon over all scats containing ants. It is important to note, that FV of ants in general (hence FV_i) refers to the average percent volume of ants over all scats analyzed in a particular season. However, FV of different ant groups and species (hence FV_a) shows their average percent of volume only among ants in particular season. FO is the percent of scats containing given food item over all scats in particular season.

Ants were counted in each subsample based on their heads and their identity was determined by an experienced myrmecologist (Dr. Ants-Johannes Martin) to the finest taxonomic level possible by using 10–80 power microscope and reference material. An average individual biomass (Tab. S1) was multiplied by the average number of ants in five subsamples to estimate percent volume of different ant species in scat. Head capsules of ants were used to estimate relative number of eaten individuals, because these body parts of ants are the most durable part. Additionally, we divided the ants into five genus groups: 1) *Formica* spp.; 2) *Camponotus* spp.; 3) *Lasius* spp.; 4) *Myrmica* spp.; and 5) *Serviformica* spp. This classification provided the best means for comparing our results to those of other European studies (e.g. Dahle et al., 1998; Swenson et al., 1999; Große et al., 2003; Stenset et al., 2016).

Ant inventory

To estimate preferences of ants by brown bears, we conducted an ant inventory in the same counties where scat collection was carried out. We determined ant species and biomass available to brown bears. Because ant activity is temperature-dependent, the data were collected only during dry and warm weather (temperature above 15 °C). In every county, two 5–10 km² plots were explored. The location of these plots was determined based on the results of bear scat collection, so that the transects were located in dietary study areas. Five long (500 m long and 20 m wide) and five short (50 m long and 2 m wide) transects were selected with a random starting point and direction on every plot in the habitat of bears (forests and their immediate surroundings). In situations where ant biomass and species composition among five selected plots/transects were remarkably heterogeneous, one to three plots/transects were additionally explored and included into analysis. On long transects we estimated biomass and species that live in mounds (*Formica* spp. mostly), whereas on short transects ants inside dead wood and underground (including *Lasius* spp.) were estimated. We summed the biomass data of short and long transects, because species studied on these two types of transects were different and therefore we treated the data as additive.

All dead wood and tufts were opened with an axe on short transects and ant colony size was visually determined (Rolstad et al., 1998). In every colony, 5–15 ants were taken to the lab for ant species determination and weighing. To evaluate biomass of a colony, the average weight

of the individual and number of individuals in the colony were multiplied. Ants were preserved frozen and weighed with an Ohaus Voyager VP64CN (± 0.1 mg).

Along long transects, the diameter and height of all red ant mounds were measured. However, to evaluate the number of ants in mound, we used the formula developed by Zahharov (1978),

$$N_e = \sum_{i=1}^n (M_i \cdot 7.7 \cdot A)$$

where N_e is number of ants in mounds, M_i is number of chemical trails and $A = 36.82 - 2.127 \cdot I + 0.112 \cdot I^2 - 0.00047 \cdot I^3$ (I : intensity of movement, measured as number of moving individuals in one direction per one minute). Number of ants in mound and weight of an individual were multiplied to estimate the biomass of the mound.

During ant inventory we also collected ants from their nests (10–20 individuals per nest) to get data of average weight considering different ant species. We additionally calculated the correlation between parameters gained from ant inventory data and data from scat analysis. In order to determine ant preferences by bears both in terms of biomass and density, we used the Ivlev's selectivity index Ivlev (1961): $E = \frac{(r-p)}{(r+p)}$, where r is the proportion of food item in diet and p is the proportion of same food item in the environment. In order to calculate preference by biomass, we used the FV_a of particular ant group and percent of corresponding biomass of that ant group based on ant inventory data. To calculate preference by density FO of particular ant group and respective percent of colonies found per hectare was used. The index values are between -1 and +1: values near -1 indicate avoidance of a particular food item, values close +1 indicate total preference, and values close to zero show that a particular food item is consumed in proportion of its availability.

Geographical variation analysis

To place the Estonian data of brown bear myrmecophagy into the European context, we used the estimated dietary content (EDC) of ants from Vulla et al. (2009). In addition, we gathered EDC data from other studies (Tab. 3). EDC is preferred over FV and FO (faecal volume and frequency of occurrence, respectively), as it reflects the actual consumption of particular food items. EDC was calculated as described in Hewitt and Robbins (1996), by multiplying the FV s of food items in scats by corresponding correction factors that were developed via feeding studies to correct for differential digestibility. Study areas were grouped into temperate or boreal zones based on Olson et al. (2001) to analyze their effects.

Statistical analysis

Mann-Whitney U-test or Kruskal-Wallis test were used to analyze statistical differences between groups of interest, depending on the number of groups. Statistical differences were considered to be significant when $p < 0.05$. Correlations between latitude and consumption of ants were calculated, as well as between seasons and zones. Statistical analyses were done using the program Statistica 7.0 (StatSoft, Inc.).

Results

Scat analysis

In total, data of 142 brown bear scats collected during 2003–2004 (spring: $n=16$; summer: $n=20$; autumn: $n=106$) (Vulla et al., 2009) were used. Of these, 73 contained ants (51.2%) (Fig. S2). FV_t of ants did not differ significantly between years ($U=2420$; $p=0.69$) or among counties at any season (Kruskal-Wallis test, spring: $H=0.1$, $df=2$, $p=0.9$; summer: $H=0.45$, $df=1$, $p=0.49$; autumn: $H=2.3$, $df=2$, $p=0.32$), so the data were pooled across years and counties for further analysis.

Altogether, 18 species of ants (Tab. 1) belonging into two subfamilies (Formicinae and Myrmicinae) and five genus/groups (*Myrmica* spp., *Lasius* spp., *Formica* spp., *Camponotus* spp., *Serviformica* spp.) were identified. The remains of *Camponotus fallax* were identified for the first time in Estonia. We could not, however, determine its abundance

Table 1 – Ant content in brown bear scats ($n=142$) collected from Estonia during 2003–2004.

Food item	Spring (n=16)			Summer (n=20)			Autumn (n=106)		
	FV	FO	EDC	FV	FO	EDC	FV	FO	EDC
Ants (all species)*	3.5**	56.3	7.4	15.7**	75	29.3	4.2**	46.2	5.2
<i>Formica</i> spp.	75.9	37.5		30	65		49.4	26.4	
<i>F. aquilonia</i>	-	-		0.1	5		6.1	3.8	
<i>F. exsecta</i>	-	-		-	-		0.5	5.7	
<i>F. polycetena</i>	35.1	18.8		6.1	15		<u>34.6</u>	<u>17</u>	
<i>F. pratensis</i>	-	-		-	-		0.1	0.9	
<i>F. rufa</i>	<u>40.9</u>	<u>25</u>		11.3	30		4.3	5.7	
<i>F. sanguinea</i>	-	-		12.6	20		3.7	3.8	
<i>Lasius</i> spp.	5.7	12.5		60.9	70		17.5	28.3	
<i>L. alienus</i>	-	-		1.0	5.0		-	-	
<i>L. flavus</i>	-	-		0.1	5		8.1	9.4	
<i>L. fuliginosus</i>	5.38	6.3		-	-		1.4	3.8	
<i>L. niger</i>	0.36	6.3		<u>54.5</u>	<u>65.0</u>		4.3	16	
<i>L. umbratus</i>	-	-		5.3	5		3.7	3.8	
<i>Camponotus</i> spp.	-	-		8.9	15		27.1	6.6	
<i>C. sp.</i>	-	-		7.9	5		27.1	6.6	
<i>C. fallax</i>	-	-		0.5	5		-	-	
<i>C. herculeanus</i>	-	-		0.5	5		-	-	
<i>Serviformica</i> spp.	18.3	6.3		-	-		2.8	14.0	
<i>S. fusca</i>	-	-		-	-		1.6	12.3	
<i>S. cinerea</i>	18.3	6.3		-	-		-	-	
<i>S. cunicularia</i>	-	-		-	-		1.2	3.8	
<i>Myrmica</i> spp.	-	-		0.02	5		3.2	13.2	
<i>M. rubra</i>	-	-		-	-		1.9	9.4	
<i>M. ruginodis</i>	-	-		0.02	5		1.3	6.6	

FV: faecal volume; FO: frequency of occurrence; EDC: estimated dietary content.

* data from Vulla et al. (2009);

** refers faecal volume of ants over all scats in particular season, whereas FV in different ant groups/species is a percent from FV of ants (FV_a). Dominating ant species in each season are underlined.

relative to other *Camponotus* species, because most often we could only identify these ants to the level of genus, as most individuals in scats were highly degraded.

Ant consumption in different season

In spring *Formica* spp. was the most common ant group ($FV_a=75.9\%$, $FO=37.5$), with two dominating species: *F. rufa* ($FV_a=40.9\%$, $FO=25\%$) and *F. polycetena* ($FV_a=35\%$, $FO=18.8\%$) (Tab. 1). *Serviformica* was the second most important ant groups in spring ($FV_a=18.3\%$), followed by *Lasius*.

The consumption of ants was highest during summer, when 75% of scats (collected during that time) contained ants, constituting 15.8% of FV_t (Tab. 1). Although *Lasius* and *Formica* ants were consumed in similar frequencies ($FO=70$ and $FO=65$, respectively) during summer, the volume of *Lasius* ants was twice the volume of *Formica* ants ($FV_a=61\%$ and $FV_a=30\%$, respectively). FV_a of Carpenter ants (*Camponotus* spp.) was 8.9%, whereas the occurrence of *Myrmica* ants was scarce and ants belonging in the *Serviformica* group were not detected during summer. Among 11 identified ant species during summer *L. niger* had the largest volume ($FV_a=54.5\%$; $FO=65$), followed by *F. rufa* and *F. sanguinea* ($FO=30$, $FV_a=11.3$, and $FO=20$, $FV_a=12.6$, respectively).

The importance of ants decreased in autumn, when their general consumption was comparable to that of springtime (Tab. 1). Nevertheless, the prevalence of different ant groups and species was different from other seasons. The proportion of *Formica* ants was the highest, with almost half of the consumed volume ($FV_a=49.4\%$). *Lasius* ants were consumed as frequently as *Formica* ants, but their volume was considerably smaller ($FV_a=17.5\%$). Although the carpenter ants were quite rare in scats ($FO=6.6\%$), their proportion of scat volume was almost one third. Therefore, they were the second most important ant group by volume in bear diet during autumn. *Myrmica* and *Serviformica* ants

were consumed in smaller quantities, although more frequently than carpenter ants. At the species level, *F. polycтена* contributed one-third of the volume, being also the most frequent species. The importance of *F. rufa* was lower compared to spring and summer, and was in comparable level with *F. aquilonia* and *F. sanguinea*. In the *Lasius* group, *L. flavus* had the largest volume ($FV_a=8.1\%$, $FO=9.4$), still *L. niger* was consumed more frequently ($FO=16$).

Ant biomass and preferences

In total 33 long and 43 short transects were explored. On 22 long (66.7%) and on one short (2.3%) transect ant colonies were not detected. Altogether, 11 species of ants were identified on transects (Tab. 2), all of them also found in brown bear scats. The average ant biomass was 7.7 kg/ha (Tab. 2). Variation in biomass between different ant groups was high, from 0.7 g/ha for *Camponotus* spp. up to 7.2 kg/ha (93.5% of biomass available) for *Formica* spp. (Tab. 2). *Formica aquilonia* and *F. polycтена* had the highest biomass and together they comprised 59.3% of all ant biomass available. The very high prevalence of *Formica* spp. in biomass relative to other species was due to the very large size of their colonies, and not to their density on the landscape. The mound-building *Formica* colonies averaged over two kg in biomass, of which *F. aquilonia* and *F. polycтена* had even more than four kg per mound, whereas other genera rarely exceed two kg per colony. Less than two *Formica* colonies occurred in one hectare of study area, whereas the number of colonies of other genera (summed) was higher than 450 per ha (Tab. 2). During the biomass analysis, single *Camponotus* colony belonging to *C. herculeanus* was found living in tree and we were able to count only 20 individuals.

Among identified species, we found significant positive correlation between colony number per hectare and FO of scats in autumn ($R=0.684$; $p<0.05$) and negative correlation between the average calculated weight of ant species and FO ($R=-0.627$; $p<0.05$) in autumn. Among other seasons, no significant correlation was detected between identified field variables and either FO or FV (data not shown).

The highest preference by bears was detected for *Camponotus* ants (Fig. 2), both in summer and in all seasons together. *Formica* ants were underrepresented in bear diet, based on FV_a relative to their biomass availability, but were strongly overrepresented in the diet based on FO relative to colony density, both in summer and whole year. By analyzing scats of the whole year, *Lasius* ants were preferred based on the available biomass, but not based on density. However, in summer *Lasius* ants were preferred both by biomass and density. According to selectivity indexes, *Myrmica* spp. was avoided by bears, especially in summer.

Myrmecophagy of Estonian brown bears in European context

Data from nine studies indicate that the EDC of ants in the diet of European brown bears is usually highest during summer and spring (Tab. 3, Fig. 3). Consumption of ants was highest in Sweden, Estonia, Italy and Slovenia, where ants contributed $\geq 25\%$ of EDC, and lowest in Slovakia and the northern part of Norway ($<9\%$). No correlation between latitude and ant consumption was detected in any season or overall (Fig. 3), and no statistically significant results were identified between the two zones. Ant consumption was more similar between zones, whereas within zones EDC of ants varied from 3.5–30% at boreal sites and 6–39.3% at temperate sites (Tab. 3, Fig. 4).

To describe the proportion of different ant groups in bear diet we could include data only from Slovenia, Estonia, Sweden and Norway (Fig. 5). Compared with Sweden and especially Norway, bears in Slovenia and Estonia consume seasonally a wider range of different ant groups (1–3 groups vs. 3–5 groups; Fig. 5). Bears in Sweden and Norway feed mostly on *Camponotus* and *Formica* (range seasonal in 88.2–100% cumulative of both species), whereas *Lasius* and *Serviformica* were consumed in considerable amount only in Slovenia (range seasonal in 57.5–66.6% cumulative of both species) and Estonia (range seasonal in 20.3–24% cumulative of both species). The consumption of *Myrmica* was highest in Sweden during summer (11.8%) and rather

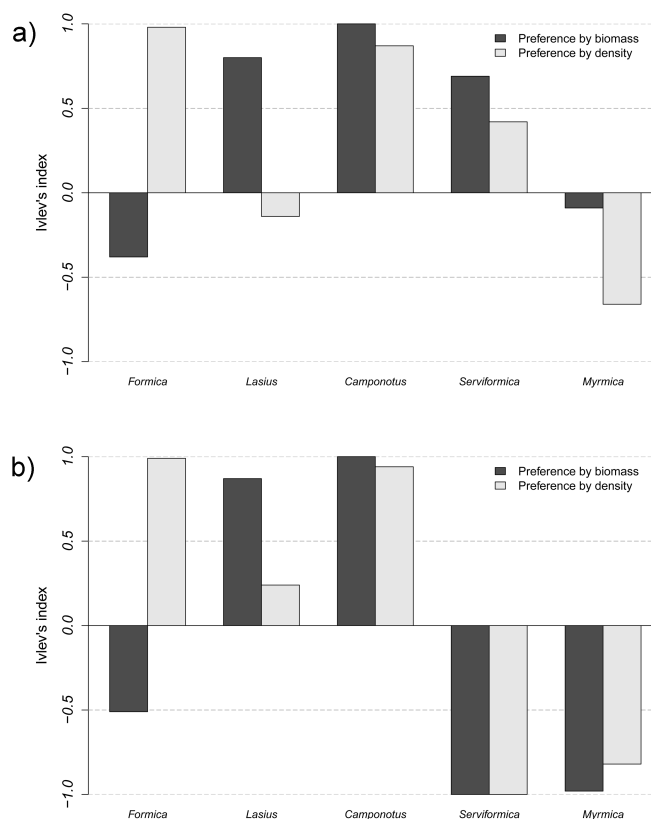


Figure 2 – Selectivity (Ivlev's index) of different ant groups by brown bears in Estonia: a) during the entire study period, b) during summer. Groups with positive value are selected while those with negative are avoided by bears.

low in Estonia (in summer 0.02% and autumn 3.2%) and Slovenia (in summer 1.1% and autumn 0.3%).

During springtime, *Formica* was the dominant ant group consumed in Slovenia, Estonia, Sweden and Norway, and their EDC increased with latitude from 39.3% in Slovenia to 100% in Norway; Fig. 5). However, in Norway bears consumed only *Formica* spp. In summer EDC of *Lasius* increased both in Slovenia and Estonia (from 26.7 to 52.11 and from 5.7 to 60.9, respectively). In Sweden the EDC of *Camponotus* ants increased from 10.5 in spring to 58.8 in summer. During autumn all five ant groups were identified in the diet of Estonian and Slovenian bears, however more than 92% of EDC consisted of three genera: *Lasius*, *Formica* and *Camponotus*.

Biomass of different ant groups available for bears in Sweden, Slovenia and Estonia were rather different (Tab. S3). *Formica* spp. represent the dominating ant group in Sweden and Estonia, with biomass over seven kilograms per hectare (FV_a of *Formica* spp.: 98.1% in Sweden and 93.5% in Estonia). In Slovenia, the available biomass of *Formica* spp. was only four grams per hectare. Based on the ant inventory in Slovenia *Lasius* ants had the highest biomass among different ant groups, yet their overall biomass was about one-fourth compared to Estonia (72 g/ha in Slovenia and 323 g/ha in Estonia). The biomass of *Lasius* ants was extremely low in Sweden (0.005 g/ha). Available biomasses of *Serviformica* and *Camponotus* ants were highest in Sweden, whereas the biomass of *Myrmica* ants was highest in Estonia.

Discussion

Ants in brown bear diet and discovery of a new species for Estonia

Our brown bear dietary analysis revealed 18 species of ants out of 51 described so far in Estonia (A.-J. Martin, unpublished data). Interestingly, our study showed that dietary analyses could help discovering new species, as remains of *Camponotus fallax* were identified for the first time in Estonia and thus elevating the number of

Table 2 – Estimated ant biomass in Estonia, survey conducted in summer 2005.

Ant species	Mound/ha (±SE)	Average number of ants in mound (±SE)	Biomass g/ha (±SE)
<i>Formica aquilonia</i>	0.6 ± 0.5	(1.3 ± 1.0) × 10 ⁶	2472 ± 1890
<i>F. exsecta</i>	0.09 ± 0.05	3300 ± 1200	29.0 ± 17.5
<i>F. polyctena</i>	0.9 ± 0.4	(7.4 ± 2.5) × 10 ⁵	4546 ± 2316
<i>F. pratensis</i>	0.06 ± 0.06	(7.5 ± 4.0) × 10 ⁴	101.4 ± 101.4
<i>F. rufa</i>	0.06 ± 0.04	2500 ± 250	16.6 ± 13.6
<i>F. fusca</i>	20.9 ± 9.1	361.1 ± 57.8	33.3 ± 14.8
<i>Lasius niger</i>	158.1 ± 38.3	891.0 ± 220.6	299.3 ± 115.5
<i>L. flavus</i>	37.2 ± 15.3	554.2 ± 259.0	23.5 ± 13.7
<i>Camponotus herculeaneus</i>	2.3 ± 2.3	20	0.7 ± 0.7
<i>Myrmica rubra</i>	96.9 ± 21.9	283.8 ± 38.1	59.7 ± 17.1
<i>M. ruginodis</i>	141.0 ± 20.3	259.0 ± 34.9	82.1 ± 15.9
Total			7663.6

ant species identified in the country up to 52. According to AntWeb (<http://www.antweb.org>, accessed 18th December 2018) this species is relatively widely distributed in Europe. However, the closest place to Estonia that this species has been found is southern Sweden, and it has not been recorded in the Baltic region, Finland and nearby Russia. *Camponotus fallax* lives in small colonies of 30–50 individuals in the trunks of dead wood in open deciduous woodlands (Collingwood, 1979), which makes it unlikely for humans to detect this species in traditional surveys. Therefore, the strong selection for *Camponotus* ants by brown bears makes it more likely to detect them during the studies of bear's eating habits.

In accordance with Swenson et al. (1999), our results show that among *Formica* species bears tend to consume species with larger mounds, rather than those that are more numerous. Among different ant groups, *Formica* ants living in large mounds prevailed in bear diet during springtime. Based on the available data, dominance of *Formica* ants in the diet during springtime seems to be typical for bears living in northern and eastern Europe (Slobodjan, 1993; Johansen, 1997; Swenson et al., 1999), as well as in some populations in central Europe (Große et al., 2003). One of the functions of a mound is accumulation of heat, so ants living in mounds activate earlier in spring compared to ground-nesting or wood-nesting species (Hölldobler and Wilson, 1990). For catching the warmth radiating from the sun, *Formica* ants concentrate in upper layers (chambers) and at the top of the mound, which makes it possible for bears to consume high amount of ants with less anthill material per time unit (Johansen, 1997).

The relatively high FV_a of *F. cinerea* (*Serviformica*) in spring might be misleading, since only one scat contained this rare ant species. However, as this species lives usually in underground nest in sunny sand habitats, they activate earlier compared with many other ant species (Maavara, 1953). The absence of *Camponotus* and *Myrmica* ants in

spring probably reflects a combination of their unavailability for bears due to later activation (Hölldobler and Wilson, 1990) and small number of scats being analysed.

Similar to our study, domination of *Lasius* in summer has been observed also in Slovenia (Große et al., 2003). However, Slovenian bears tend to consume *Lasius* ants in larger quantities also in spring and autumn compared to their Estonian counterparts. In our study, the importance of *Lasius* ants (mainly *L. niger*) increased substantially during summer and although they were consumed as frequently as *Formica* ants, their volume was twice as high. Thus, it seems that during summer the average biomass of ants consumed per excavated ant nest is higher when bears feed on *Lasius* as compared to *Formica* ants. In a study conducted in central Italy it was found also that during summer-months *Lasius* and *Formica* ants were consumed in similar frequency (Tosoni et al., 2018). In light of previous discussion, we can conclude that *FO* may be good indicator of visited habitats, yet poorly reflecting nutritional contribution of different ant species/groups. *Lasius* ants are smaller than *Formica* or carpenter ants, but their colonies are more abundant. Additionally, there may be some nutritional advantages by favoring *Lasius* ants over the other ant groups. For example, *Lasius* ants seem to have higher content of fat compared to *Formica* and *Camponotus* (Swenson et al., 1999; Auger et al., 2004; Yamazaki et al., 2012). Larger colonies of *Lasius* ants during summer, combined with their nutritional value and gentle behavior, apparently resulted in higher preference of *Lasius* during this period.

The black garden ant (*Lasius niger*), one the most common species in Estonian agricultural and natural landscapes, was dominant in bear diet during summer. The nest type of *L. niger* depends on habitat characteristics, since the species lives inside rotting tree trunks at forested areas, but in open areas these ants build mounds, which can be as high as 60 cm (Maavara, 1993) and are therefore visually well detected. As

Table 3 – Estimated dietary content (EDC) of ants in various European brown bear dietary studies.

Reference	Location	Zone	Latitude	Study period	n	EDC		
						Spring	Summer	Autumn
1. Ciucci et al., 2014	Italy	Temperate	41.5	2006–2009	2359	2.4	27.6	2.45
2. Große et al., 2003	Slovenia	Temperate	46	1997–1998	200	4.2	25	5.3
3. Rigg and Gorman, 2005	Slovakia	Temperate	49	2001–2003	373	1.3	6.4	1
4. Stofik et al., 2013	Slovakia	Temperate	49	2008–2010	215	9	6	0
5. Vulla et al., 2009	Estonia	Temperate	58	2003–2004	142	7.4	29.3	5.2
6. Johansen, 1997	Sweden	Boreal	61	1994–1995	234	38	30	7
7. Dahle et al., 1998	Sweden	Boreal	64	1987–1988, 1993–1995	148	14.5	28	5
8. Dahle et al., 1998	Norway	Boreal	64	1987–1988, 1993–1995	118	17.5	3.5	12
9. Persson et al., 2001	Norway	Boreal	69	1978–1982	137	2.5	7.9	3.8

Numbers in front of the references are in accordance with numbers in Fig. 3.

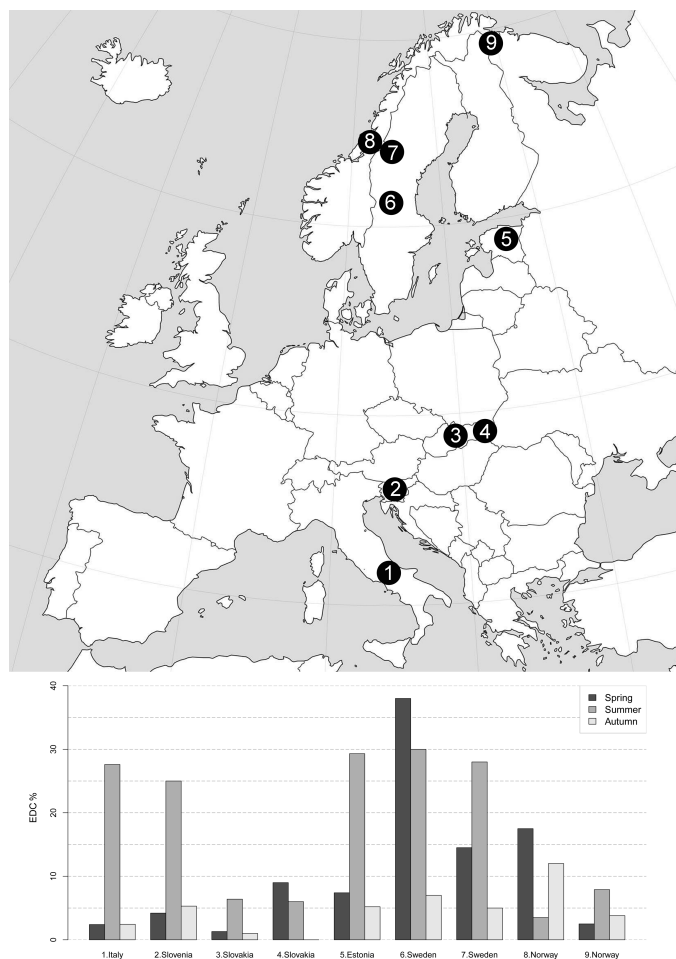


Figure 3 – European map in above shows the location of study areas in reviewed papers (see Tab. 3 for details), numbered as follow: 1. Ciucci et al. (2014), 2. Große et al. (2003), 3. Rigg and Gorman (2005), 4. Stofik et al. (2013), 5. Vulla et al. (2009), 6. Johansen (1997), 7. Dahle et al. (1998) (in Swedish part of the study area), 8. Dahle et al. (1998) (in Norwegian part of the study area), 9. Persson et al. (2001). Graph below: Estimated dietary content (EDC) of ants in bear diet in the above mentioned study areas (numbers below graph correspond to numbers in the map) considering different seasons: spring, summer, autumn.

the biomass of pupae is highest in summer (Swenson et al., 1999) and the colony densities of *L. niger* can be quite high at least in some habitats, bears can move among the nests to consume more ants per time unit (Fujiwara et al., 2013). The escape time of *Lasius* ants is longer when there are many pupae in the nest (Yamazaki et al., 2012) and as workers tend to concentrate to carry pupae away they are easy catch for bears.

The largest numbers of scats were collected during autumn and this can be one of the reasons, why the number of ants taxa identified was largest during that period (14 species and additionally *Camponotus* spp.). However, in autumn, the amount of ants in bear diet declined as bears tended to eat mainly carbohydrates rich food items as berries, apples and cereals in Estonia (Vulla et al., 2009). Before hibernation, maximization of energy intake to accumulate fat reserves is especially important for bears. It has been suggested that the rate of gain is in maximum when dietary protein content constitute slightly less than one-fifth of the dry matter content (Robbins et al., 2007; Erlenbach et al., 2014). During autumn, bears are able to optimize their diet by mixing carbohydrate-rich items with other food like ants, ungulates or green vegetation (Coogan et al., 2014).

Which ant species bears prefer?

Our estimation of available ant biomass (7.7 kg/ha) was comparable to that in Sweden (9.6 kg/ha; Swenson et al., 1999) and much higher compared to Slovenia (0.135 kg/ha; Große et al., 2003). In our ant inven-

tory, we identified 11 species, which represent 61% of species discovered from bear scats. Interestingly, despite of high available biomass of *F. aquilonia*, its contribution based on scat analysis was rather low. This species is most abundant in old forests (Kilpeläinen et al., 2008)), which are not widely distributed in our study area. As in Scandinavia this particular species often dominates in bear diet (Elgmork and Unander, 1999; Swenson et al., 1999), we presume that bears in Estonia also consume this species when available.

Whereas *Formica* and *Lasius* spp. were the most consumed ant groups by brown bears in Estonia, the carpenter ants (*Camponotus*) were highly favored and *Myrmica* spp. were avoided. Thus, Estonian bears tend to follow the general pattern identified in other bear studies (Noyce et al., 1997; Swenson et al., 1999; Mattson, 2001; Große et al., 2003). Colonies of *Myrmica* ants are small and located inside the ground, being visually hard to detect. Moreover, the small body size, aggressive behavior, high formic acid content and the presence of stinger (Hölldobler and Wilson, 1990) might deter bears. Bears prefer carpenter ants to the *Formica* ants despite the larger nests of the latter genera, probably because they contain more fat and less formic acid, and have larger body size with higher nutritional value (Johansen, 1997; Swenson et al., 1999; Mattson, 2001; Große et al., 2003). On the other hand, colonies of carpenter ants are relatively small, located sparsely and their biomass is therefore smaller compared to other ant groups, thus carpenter ants are often consumed in lower volumes despite their nutritional advantages.

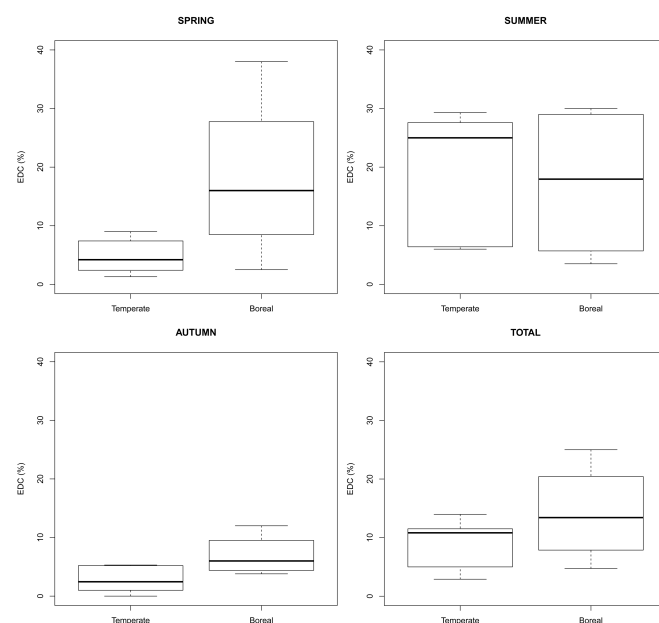


Figure 4 – Percentage of Estimated Dietary Content (EDC) of ants in brown bear diet in temperate and boreal zones, based on data of literature (see Tab. 3 for details). Inner boxplot lines are median values, box margins are 25th and 75th percentiles, whiskers are 5th and 95th percentiles.

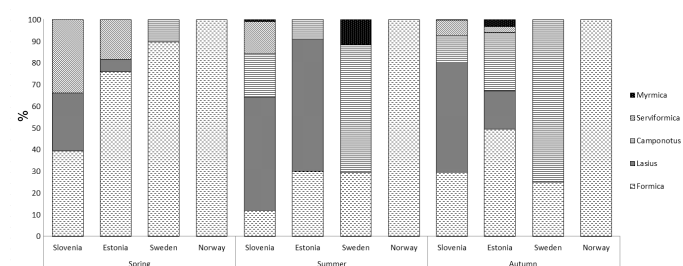


Figure 5 – Proportion of different ant groups (FV) in bear scats in Slovenia (Große et al., 2003), Estonia (this study), Sweden (Johansen, 1997) and Norway (Persson et al., 2001).

Patterns of myrmecophagy in Estonian and other European brown bears

As in most other regions, ants are important food items in Estonian bear diet especially during summer, when they contribute almost 30% of EDC (Vulla et al., 2009). This is comparable with the estimates for bears in Sweden (Johansen, 1997; Dahle et al., 1998), Italy (Tosoni et al., 2018) and Slovenia (Große et al., 2003).

Highest consumption of ants in various brown bear populations occurs either during spring (Mordosov, 1993; Johansen, 1997; Dahle et al., 1998) or more often during summer (e.g. Mattson et al., 1991; Clevenger et al., 1992; Swenson et al., 1999; Rigg and Gorman, 2005; Vulla et al., 2009; Paralikidis et al., 2010; Ciucci et al., 2014). Even high availability of other high-energy food at supplemental feeding sites does not change the peak consumption of ants in summer (Große et al., 2003; Vulla et al., 2009). This indicates that at least seasonally, ants are not merely a secondary food resource, but a highly valued dietary component.

During summer, when the fiber content of plant food increases and the digestibility and energy content decreases (Pritchard and Robbins, 1990; Noyce et al., 1997), ants are favored as a source of energy-rich food (López-Alfaro et al., 2015). The increase of ant consumption in summer coincides with the peak availability of pupae in nests (Swenson et al., 1999; Noyce et al., 1997). It is reasonable to assume that the higher digestibility, and lack of defense mechanisms of pupae makes them an easy target for bears (Auger et al., 2004) and may trigger the ant feeding (Fujiwara et al., 2013).

As the preference patterns of bears for different ant groups and species seem to be universal, the regional differences in ant consumption are most likely affected by local availability (Noyce et al., 1997). However, the average available biomass can be quite a poor predictor of consumption, as the variation of ant biomass can be highly variable in different areas and bears tend to have good memory for locating food (Selva et al., 2017). For example, Große et al. (2003) found that in daybed plots the ant biomass extensively exceeded the average biomass, especially when considering the preferred species.

Ants are an important component in the diet of many European brown bear populations and at least in some, a highly significant source of protein (Ciucci et al., 2014; Costello et al., 2016; Stenset et al., 2016). Higher level of digestible protein available in ecosystems is correlated with higher reproductive rate in a brown bear populations (López-Alfaro et al., 2015). Thus, among other natural food items, ants should be considered as a key food category in the brown bear diet. Brown bears make specific effort to find ants and display strong preferences for certain species, even within the same genus. Seasonal changes in the ant species consumed by bears within our study area appears to reflect both preference and seasonal progression in the availability of different ant species and, perhaps, their pupae. Brown bears across Europe, and around the world's temperate zones, seem to display similar preferences for specific ant genera and species. Across Europe, the main differences appear to reflect primarily the availability of preferred types of ants and/or the habitats that they live in. This rule seems to be general across all bears living in the temperate zone. Similar to Europe, brown bears in North-America consume ants in highest proportion in summer (Munro et al., 2006), although in smaller quantities (Munro et al., 2006; Costello et al., 2016). Consumption of ants, mostly of genera *Formica* and *Lasius* (Fujiwara et al., 2013; Noyce et al., 1997; Auger et al., 2004), also peak in summer, but are eaten even in larger quantities by American black bear and Asiatic black bear (Noyce et al., 1997; Costello et al., 2016; Lesmerises et al., 2015; Fujiwara et al., 2013), which makes ants an important diet item for different bear species. Overall importance of ants in the diet of bear species urge to use management techniques in bear habitat (e.g. higher proportion of dead wood, less disruption of soil) that tend to favor occurrence, density, and diversity of ant species available to bears. ☞

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Supplemental information

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

Supplemental Table S1 Average biomass of individuals sampled in Estonia.

Supplemental Figure S2 Correlation between latitude and percentage of Estimated Dietary Content of ants in the diet of brown bears.

Supplemental Table S3 Estimated biomass of ants available for bears in Sweden, Slovenia and Estonia.