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Ants as food for Apennine brown bears

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Abstract

The value of ants to bears is a topic of substantial relevance for the small and highly endangered population of Apennine brown bears (*Ursus arctos marsicanus*) in central Italy. Following a previous food-habit study (2006–2009) based on scat analysis, we used the same data set to further investigate patterns of ant consumption by Apennine bears at a greater taxonomic and temporal resolution. We observed a great diversity of ant species in bear scats, comprising 15 genera and > 42 species. Bears most frequently consumed ants living in open grassland and forest edges, belonging to five genera: *Formica*, *Lasius*, *Tetramorium*, *Camponotus* and *Myrmica*. Specifically, yellow *Lasius* spp., *Serviformica* spp., *Lasius* s. str. spp., and *Tetramorium* spp. were most represented in the bear diet, followed by *Formica pratensis*, *Camponotus* spp., *Myrmica* spp. and *Formica sanguinea*. Yellow *Lasius* spp. yielded the highest number of individuals per bear scat, outnumbering any other ant taxon. During the years of our study, ant consumption by bears peaked between June and July and corresponded to a higher occurrence of brood in the scats. Our results are useful to inform habitat management, especially in light of expected natural and anthropogenic changes. However, further investigation is necessary to unveil behavioural and ecological correlates of myrmecophagy in Apennine brown bears.

Keywords: *Apennine brown bear*, *myrmecophagy*, *food habits*, *Ursus arctos marsicanus*, *ants*

Introduction

Although bears are large carnivorous mammals, their diet is diverse and comprises a conspicuous share of vegetable matter (fruits, leaves, stems, roots), varying markedly along a latitudinal gradient and according to prevailing environmental conditions (Bojarska & Selva 2012). Ants represent a consistent, quite stable and easily accessible food source for bears (Gunther et al. 2014; Costello et al. 2016). Due to their macronutrient balance (Coogan et al. 2014; Erlenbach et al. 2014) and essential amino acid contents (Redford & Dorea 1984; Noyce et al. 1997), ants are believed to compensate for seasonal nutrition deficiencies (Noyce et al. 1997; Swenson et al. 1999), increase efficacy of mass gain, and contribute to maintaining lean body mass and fat stores (Coogan et al. 2014; Erlenbach et al. 2014). In particular, adult female and young bears, due to their smaller size and limited intake rate

(Hilderbrand et al. 1999), are expected to benefit the most from consuming ants, whose nutritional contribution may therefore be critical for reproductive success (Bull et al. 2001; López-Alfaro et al. 2013).

Myrmecophagy has been reported both in black (*Ursus americanus*; Noyce et al. 1997; Costello et al. 2016) and brown (*Ursus arctos*; Swenson et al. 1999; Mattson 2001) bears, and brown bears in Europe are no exception (Elgmork & Kaasa 1992; Swenson et al. 1999; Große et al. 2003; Kavčič et al. 2015; Stenset et al. 2016). According to these studies, bears consume ants essentially during spring and summer, likely as a response to the increased availability of ants and brood in their nests (Noyce et al. 1997; Auger et al. 2004; Fujiwara et al. 2013). Bears appear to consume ants selectively (Noyce et al. 1997; Große et al. 2003; Yamazaki et al. 2012; Fujiwara et al. 2013) with foraging efficiency driving

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ant species selection (Noyce et al. 1997; Swenson et al. 1999; Mattson 2001; Auger et al. 2004).

In a recently conducted dietary study on Apennine brown bears, ants were estimated to provide an average of 35.7 (\pm 0.1 standard deviation, SD)% of digestible energy in June–July, when their consumption by bears was highest (Ciucci et al. 2014). Complementing that work, and using the same sample of bear scats (Ciucci et al. 2014), we describe here patterns of ant consumption by Apennine brown bears at a greater taxonomic and temporal resolution. Specifically, we: (i) assess the relative importance of ant families and genera in the bear diet, (ii) report the seasonal phenology in the relative consumption of the most frequently consumed ants, and (iii) describe the seasonal variation in dietary ant caste composition (i.e. adults vs brood).

Study area

We conducted our study in the Abruzzo, Lazio and Molise National Park and adjacent areas (PNALM, 1300 km²). The elevation ranges from 986 to 2249 m above sea level, and the area is typically mountainous with rough topography, offering a variety of bear habitats, from sub-alpine meadows to low-elevation grasslands. Deciduous forests (mostly *Fagus sylvatica* and *Quercus* spp.) cover about 56% of the study area. At least 65 species of ants are known to be present in the PNALM area (M. Mei, unpublished data), although no systematic ant survey has been conducted locally. Further details on the study area can be found in Ciucci et al. (2014, 2015).

Materials and methods

Using a sample of 2539 bear scats collected in the PNALM from June 2006 through December 2009 (Ciucci et al. 2014), we focused our analyses on the period of highest ant consumption (June–September; Ciucci et al. 2014) to estimate the relative share of different taxonomic groups on a monthly basis. Scats were collected throughout the study area at 1–2-week intervals, and only fresh and unweathered scats were collected. Stored at -20°C until processed, bear scats were rinsed under tap water through a set of two sieves (mesh sizes 0.8 and 0.1 mm) to manually separate the different food items. Using a 7–30 \times stereoscope, a single experienced entomologist (MM) identified ants recovered in the bear scats based on morphologic differences (Noyce et al. 1997; Auger et al. 2004). Although in 2006 we limited taxonomic resolution to the genus level, we reached the lowest recognisable taxonomic level in the other years of study. When recognition at the species level was not possible, we referred to groups of species, pooling

ants that were ecologically, ethologically and morphologically distinguishable from other species of the same genera (Noyce et al. 1997). Only for scats collected in 2009, we ranked the relative abundance of ant groups in each scat according to five classes based the counts of head capsules (class 1: 1–2 capsules; 2: 3–5 capsules; 3: 6–9 capsules; 4: 10–20 capsules; 5: >20 capsules). In addition, we also defined as “prevalent” those ant species or groups occurring with \geq 10 individuals in each sample. and “dominant” ant species with the largest number of head capsules.

For each month from June–September, we quantified the relative abundance of each taxonomic group using the frequency of occurrence (FO), computed as the proportion of scats containing a given taxonomic group of ants over the total number of scats containing ants. To investigate the relationship between relative abundance of ants (response variable) and phenology (year or month as fixed factors), we used generalised linear models with Poisson and log link functions (R Core Team 2016), with the total number of ants as the offset variable to take into account differences in sample size. We also computed the relative faecal volume (FV) as the sum of the volumetric proportions of a given item divided by the total number of scats containing ants, and the importance volume (IV), as the product of FV and FO (Mealey 1980). Using POPTOOLS (version 3.2.5; Hood 2011), we then tested for month and year effects in dietary ant caste composition (i.e. brood vs adults) by means of contingency analysis based on FO, and accounted for sampling variability through a randomised χ^2 test ($n = 10,000$ simulations) with an 80% threshold (Reynolds & Aebischer 1991). We also repeated the same test of association based on FV using the Kruskal–Wallis test.

Results

Overall, we analysed 491 scats containing ants, ranging from 86 in 2006 to 150 in 2009. We found that bears consumed at least 15 genera and 24 groups of species, corresponding to at least 42 species of ants (Table I). The bulk of ants consumed by bears were represented by five genera, with *Formica* and *Lasius* occurring in 72.3% (\pm 13.8 SD) and 69.0% (\pm 23.8 SD) of scats containing ants, respectively, followed by *Tetramorium* (41.5 \pm 14.2%), *Camponotus* (23.4 \pm 6.9%) and *Myrmica* (19.1 \pm 7.8%) (Table II; Figure 1). At a greater taxonomic resolution, yellow *Lasius* spp., *Serviformica* spp., *Lasius* s. str. spp., and *Tetramorium* spp. were the most frequently consumed compared to other groups, followed by *Formica pratensis*, *Camponotus* spp., *Myrmica* spp. and *Formica sanguinea* (Table II). We did not find any annual

Table I. List of genera, species and species groups of ants identified in 491 Apennine brown bear (*Ursus arctos marsicanus*) scats collected in the Abruzzo, Lazio and Molise National Park (PNALM), Italy (June 2006–September 2009).

Subfamily	Genus	Species/group	Minimum no. of species in the study area ^a
Dolichoderinae	<i>Tapinoma</i>	spp.	1–2
Myrmicinae	<i>Aphaenogaster</i>	<i>subterranea</i>	
	<i>Crematogaster</i>	<i>scutellaris</i>	
	<i>Solenopsis</i>	<i>fugax</i>	
	<i>Messor</i>	<i>capitatus</i>	
	<i>Messor</i>	<i>structor</i>	
	<i>Myrmecina</i>	<i>graminicola</i>	
	<i>Myrmica</i>	spp.	≥ 5
	<i>Pheidole</i>	<i>pallidula</i>	
	<i>Strongylognathus</i>	sp.	
	<i>Temnothorax</i>	sp.	
Formicinae	<i>Tetramorium</i>	spp.	≥ 2
	<i>Camponotus</i>	<i>aethiops</i>	
	<i>Camponotus</i>	<i>lateralis</i>	
	<i>Camponotus</i>	<i>ligniperda</i>	
	<i>Camponotus</i>	<i>piceus</i>	
	<i>Camponotus</i>	<i>vagus</i>	
	<i>Formica</i>	<i>pratensis</i>	
	<i>Formica</i>	<i>sanguinea</i>	
	<i>Formica</i>	“ <i>Serviformica</i> ”	<i>F. cinerea</i> <i>F. clara</i> <i>F. cunicularia</i> <i>F. fusca</i> <i>F. gagates</i> <i>F. lemani</i> <i>F. rufibarbis</i>
	<i>Lasius</i>	<i>fuliginosus</i>	
	<i>Lasius</i>	“Yellow <i>Lasius</i> ”	<i>L. bicornis</i> <i>L. distinguendus</i> <i>L. meridionalis</i> <i>L. myops</i>
	<i>Lasius</i>	<i>sensu strictu</i>	<i>L. emarginatus</i> <i>L. niger</i> <i>L. paralienus</i> <i>L. platythorax</i> <i>L. psammophilus</i>
	<i>Polyergus</i>	<i>rufescens</i>	

^aMinimum number known and whose occurrence in the PNALM has been verified by focused field surveys (M. Mei, unpublished data).

effect on the relative consumption of different ant groups consumed by bears. However, on a monthly basis, consumption of yellow *Lasius* spp., *Lasius* s. str. spp., and *Camponotus* spp. decreased markedly from July to August ($P < 0.001$). In 2009, when we counted the number of ants in each scat ($n = 136$ scats with ants), yellow *Lasius* spp. was the most prevalent, yielding the highest number of individuals per scat; yellow *Lasius* spp. also outnumbered any other ant taxon in $> 60\%$ of bear scats (Table III). Consistent with seasonal occurrence, *Serviformica* spp., *Lasius* s. str. spp. and *Tetramorium* spp. ranked higher

compared to other ants in term of prevalence and dominance. *Formica pratensis*, *Camponotus* spp., *Myrmica* spp. and *Formica sanguinea* were comparable to each other in term of occurrence, but *F. pratensis* outnumbered the others, whereas *Camponotus* spp. and *Myrmica* spp. were rarely dominant in the bear scats.

In terms of importance value (IV), adult ants predominated over brood in bear scats and were consumed similarly across June–September (86.3 ± 9.5 SD %). Differently, brood peaked in June and July (21.6 ± 3.4 SD %) and decreased in August and September (5.7 ± 1.9 SD %); this trend was confirmed in terms of FO (2009 only: $\chi^2 = 16.06$, $df = 3$, significant bootstrap tests $> 91\%$) and FV (2007 and 2009: Kruskal–Wallis test = 14.76 – 46.04 , $df = 3$, $P < 0.05$).

Discussion

Ant consumption by Apennine bear during summer (Ciucci et al. 2014) was comparable to the highest levels recorded in other brown bear populations (Große et al. 2003; Bojarska & Selva 2012; Kavčič et al. 2015; Stensen et al. 2016). Ants are intensively consumed by bears in boreal forests where availability is highest (Stenset et al. 2016), but also in beach forests at lower latitudes that are highly interspersed with clearings, as a high degree of landscape diversity is advantageous for most ant species (Große et al. 2003). Although we did not quantify relative ant abundance and availability in the PNALM, ant consumption by Apennine bears likely reflects a rich ant community in our study area. This is likely associated with a marked variety of ecological conditions in the park and the widespread interspersed of forests with shrublands and open areas (e.g. clearings, meadows, pasturelands, forest, cultivated areas). In particular, Apennine bears seem to consume more frequently ants living in open grassland and forest edges. Ant accessibility may also be a relevant factor, as indicated by the high consumption by Apennine bears of *Formica* and *Lasius*, two genera often consumed by other myrmecophagous mammals as well (Redford 1987). The yellow *Lasius* sometimes build nest mounds in high densities and form large underground colonies (Noyce et al. 1997; Steinmeyer et al. 2012); they may also be attractive to bears due to their low evacuation time and attractive pheromones (Noyce et al. 1997). Consistently, yellow ants were the most frequently consumed ant species by bears also in Slovenia and Minnesota (up to 78–85% of frequency in summer; Noyce et al. 1997; Große et al. 2003;

Table II. Mean (\pm standard deviation) annual values of percentage frequency of occurrence (FO) of ant species groups detected in 491 Apennine brown bear (*Ursus arctos marsicanus*) scats collected in the Abruzzo, Lazio and Molise National Park, Italy (June 2006–September 2009). Groups of species are ranked according to FO in June. For species or groups of species, mean FO values refer to 2007–2009 only, as in 2006 ants were identified only at the genus level.

Species group	June (5–28 scats)		July (17–56 scats)		August (15–47scats)		September (9–16 scats)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Lasius</i> s. str. spp.	66.7	± 13.0	53.5	± 14.0	35.3	± 1.7	5.5	± 5.6
“Yellow <i>Lasius</i> ” spp.	52.8	± 2.6	71.9	± 6.1	48.7	± 12.0	33.0	± 19.6
<i>Lasius fuliginosus</i>	3.4	± 3.3	13.6	± 3.0	7.4	± 5.6	5.5	± 5.6
<i>Serviformica</i> spp.	51.4	± 15.5	57.7	± 12.5	43.0	± 23.0	73.5	± 20.3
<i>Formica sanguinea</i>	23.0	± 5.0	22.4	± 4.0	13.1	± 6.3	11.0	± 0.3
<i>Formica pratensis</i>	19.3	± 10.6	36.9	± 3.6	38.7	± 16.3	19.9	± 7.9
<i>Tetramorium</i> spp.	42.8	± 18.5	58.1	± 6.4	41.7	± 3.9	23.5	± 17.2
<i>Camponotus</i> spp.	24.9	± 6.3	32.5	± 14.4	18.7	± 9.1	17.4	± 12.8
<i>Myrmica</i> spp.	20.7	± 9.0	28.0	± 8.8	18.6	± 2.5	9.0	± 11.6
<i>Aphaenogaster</i> spp.	16.3	± 13.5	12.5	± 10.0	6.4	± 0.2	4.1	± 5.6
<i>Strongylognathus</i> spp.	5.0	-	1.3	± 3.1	-	-	-	-
<i>Oreinatogaster</i> spp.	4.2	± 6.9	2.7	± 6.2	-	-	-	-
<i>Messor</i> spp.	3.5	± 5.2	1.7	± 3.4	0.6	± 1.3	4.7	± 6.1
<i>Polyergus rufescens</i>	0.9	± 2.1	-	-	-	-	-	-
<i>Tapinoma</i> spp.	-	-	2.4	± 2.7	-	-	-	-
<i>Solenopsis</i> spp.	-	-	0.4	± 1.0	-	-	-	-
<i>Temnothorax</i> spp.	-	-	0.4	± 1.0	-	-	-	-

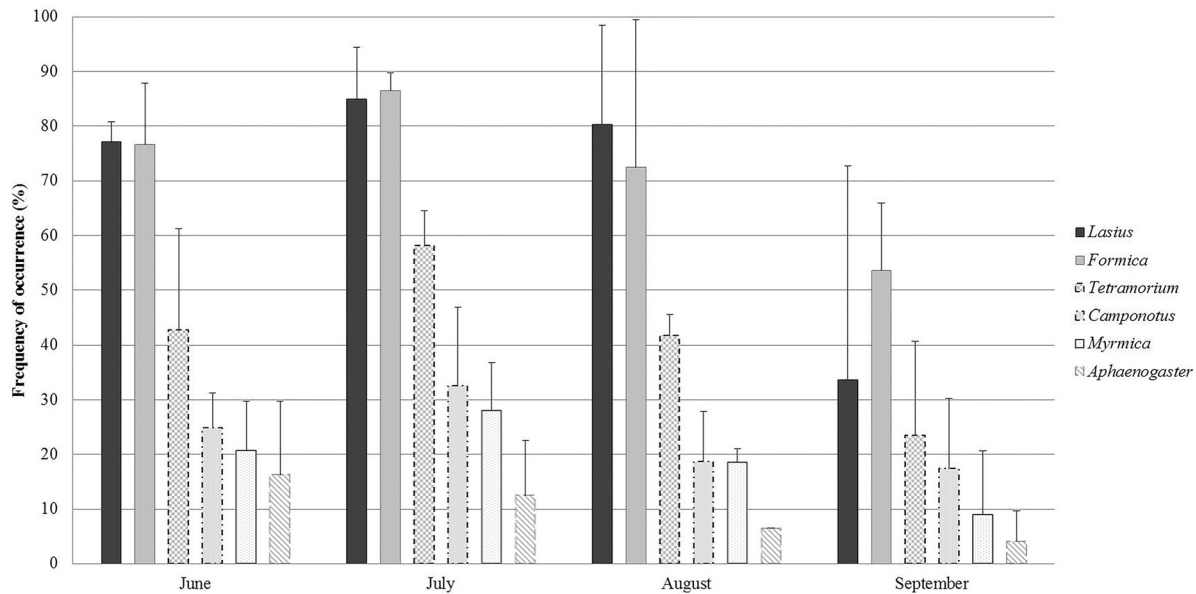


Figure 1. Seasonal changes in frequency occurrence of the six main ant genera found in 491 Apennine brown bear (*Ursus arctos marsicanus*) scats collected in the Abruzzo, Lazio and Molise National Park, Italy (June 2006–September 2009). Vertical lines above the bars indicate the standard deviation.

Table III. Occurrences of ant species groups based on the number of individuals (e.g. head capsules) found in a subsample of 136 Apennine brown bear (*Ursus arctos marsicanus*) scats collected in the Abruzzo, Lazio, and Molise National Park, Italy (June–September 2009). Groups of species are ranked according to dominance.

Species group	No. of total occurrences	Prevalence ^a	Dominance ^b
“Yellow <i>Lasius</i> ”	70	57.1	61.4
<i>Serviformica</i> spp.	78	37.1	24.3
<i>Lasius</i> s. str. spp.	84	32.1	19.0
<i>Tetramorium</i> spp.	66	34.8	18.2
<i>Aphaenogaster</i> spp.	17	17.6	17.6
<i>Formica pratensis</i>	40	32.5	17.5
<i>Formica sanguinea</i>	29	17.2	10.3
<i>Myrmica</i> spp.	44	11.3	4.5
<i>Camponotus</i> spp.	27	22.2	3.7
<i>Messor</i> spp.	1	0.0	0.0
<i>Crematogaster</i> spp.	5	20.0	0.0
<i>Solenopsis</i> spp.	1	0.0	0.0
<i>Temnothorax</i> spp.	1	0.0	0.0
<i>Strongylognathus</i> spp.	3	0.0	0.0
<i>Lasius fuliginosus</i>	12	8.3	0.0
<i>Poliergus rufescens</i>	2	0.0	0.0
<i>Tapinoma</i> spp.	1	0.0	0.0

^aPercentage of scats with ≥ 10 head capsules.

^bPercentage of scats with the largest number of head capsules.

Kavčič et al. 2015). We found that yellow ants consistently ranked high in the Apennine bear diet, not only in terms of occurrence throughout the summer, but also in terms of abundance in

each bear scat. Likely reflecting the widespread occurrence of yellow ants in our study area (Mei, unpublished data), this may also indicate that bears tend to feed longer on single large nest mounds instead of moving from one nest to another (Noyce et al. 1997; Fujiwara et al. 2013). The genus *Formica* may be highly attractive for bears, as many species of the genus form large mounds (Noyce et al. 1997; Swenson et al. 1999; Mattson 2001; Große et al. 2003). Consistently, ants of the genus *Formica* ranked high in the Apennine bear diet in terms of occurrence; several *Formica* species forming mounds or large, underground colonies ranked high also in terms of abundance in each bear scat (e.g. *Serviformica* spp., *Formica pratensis* and *Formica sanguinea*). The consumption of *Tetramorium* and *Myrmica* by Apennine bears may reflect their wide distribution in the Apennines (Sanetra et al. 1999; Radchenko & Elmes 2010), with the former occurring in large and dense colonies (Baroni-Urbani 1969). *Lasius fuliginosus* and *Aphaenogaster subterranea* were nearly the only forest species of ants consumed by Apennine bears, though they ranked lower than other ant groups. *Camponotus* comprises the most common and widely distributed forest ants in the world (Redford 1987). Because these species commonly colonise spruce and fir trees, their substantial consumption by bears has been essentially documented in northern Europe (Swenson et al. 1999; Stenset et al. 2016) and in North America

(Mattson 2001). Because the forests in the PNALM are mostly deciduous, we believe the *Camponotus* ants consumed by bears were likely associated with open environments where they nest under stones or in the ground (i.e. *Camponotus aethiops*).

At our latitude, early summer marks the beginning of the reproductive period of ant colonies, and coincides with a change in colony structure and the appearance of large masses of brood (Mei, unpublished data). Therefore, the peak occurrence of brood in the bear scats marks the peak in the consumption of ants by Apennine bears, suggesting brood might trigger ant foraging by bears, as also reported in other studies (Noyce et al. 1997; Swenson et al. 1999; Große et al. 2003; Stenset et al. 2016). However, Apennine bears consumed ants through the autumn, suggesting that adult ants are comparatively important dietary components as well (Noyce et al. 1997; Mattson 2001; Fujiwara et al. 2013). Because several additional quality foods (i.e. fruits, wild ungulates and, following mast years, hard mast; Ciucci et al. 2014) are available to Apennine bears during summer, we believe ants do not represent a secondary food item due to the lack of other seasonal key foods for bears.

Many factors affect composition and distribution of ant species, including natural succession (Costa et al. 2010), climatic change (Kwon et al. 2014) and other anthropogenic impacts on forest ecosystems (e.g. logging and livestock grazing; Schmidt et al. 2012; Frank et al. 2015). As most ant species used by Apennine brown bears are found in open and sun-exposed sites, forest clearings, early stages of forest succession, grasslands and ecotones should be actively managed accordingly. Although breeding and foraging in ants are highly affected by microclimatic factors such as insolation, herb layer cover, biomass and depth of the leaf litter, distance to forest, soil temperature and humidity (Seifert & Prosche 2017), ants are known to respond strongly to habitat changes that characterise ecological succession (Wike et al. 2010). Accordingly, we recommend that the PNALM authority promote silvicultural practices aligned with natural disturbance regimes to enhance ant species richness in the long term (Punttila et al. 1994; Franklin et al. 2002). We also suggest that productivity of ants be carefully considered within bear monitoring programmes and habitat conservation planning. Further research on myrmecophagy by Apennine bears is needed to investigate ant consumption patterns accounting for their relative abundance, accessibility and nutritional value, as this may also reveal possible cascading effects at community level (e.g. Noyce et al. 1997; Mattson 2001; Grinath et al. 2015).

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Disclosure statement

No potential conflict of interest was reported by the authors.

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