

Bears and ants: myrmecophagy by brown bears in central Scandinavia

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Abstract: To determine general patterns of myrmecophagy in bears, we tested hypotheses regarding selection of ant species, factors important to bears when selecting ant species, factors influencing seasonal use of ants, and foraging behavior of brown bears (*Ursus arctos*) in central Sweden. Ants were an important food for these bears, constituting 12, 16, and 4% of fecal volume in spring, summer, and autumn, respectively. Ants were abundant, 30.5–38.5 tonnes per bear, and bears excavated 8–33% (mean 23%) of the mounds of red forest ants annually. Carpenter ants (*Camponotus herculeanus*) were highly preferred. Among mound-building red forest ants, the *Formica aquilonia/polyctena* complex was preferred over *Formica exsecta* and *Formica lugubris*. The ants selected by bears had high digestible energy and low formic acid content and behaved passively when the colony was disturbed. Colony size and density may also have influenced the selection of ants. Seasonal use of ants was related not to the availability of pupae or the quality of plant foods but probably to the availability of other foods. Bears consumed only a small proportion of the ants, 4000–5000, each time they opened a mound, probably because of rapidly increasing difficulty in capturing them after the colony was attacked. Eurasian brown bears feed more on ants than North American bears do, perhaps because of greater availability of large colonies of red forest ants. Carpenter ants may have been especially available in our study area following intensive clear-cutting.

Résumé : Pour évaluer les patterns généraux de myrmécophagie chez les ours, nous avons éprouvé diverses hypothèses sur la sélection d'espèces particulières de fourmis et examiné les facteurs qui déterminent le choix des espèces, les facteurs qui influencent la consommation saisonnière des fourmis et le comportement de quête de nourriture des Ours bruns (*Ursus arctos*) dans le centre de la Suède. Les fourmis sont une importante source de nourriture pour ces ours, constituant 12% du volume de nourriture au printemps, 16% en été et 4% en automne. Les fourmis sont abondantes, 30.5–38.5 tonnes par ours, et les ours sondent 8–33% (moyenne 23%) des monticules construits dans les forêts par les fourmis rouges chaque année. Les fourmis charpentières (*Camponotus herculeanus*) sont de loin les fourmis préférées. Parmi les espèces qui construisent des monticules les fourmis du complexe *Formica aquilonia/polyctena* sont préférées à *F. exsecta* ou *F. lugubris*. Les fourmis préférées par les ours ont un contenu élevé en énergie digestible, un contenu faible en acide formique et leur comportement reste passif lors de perturbations de la colonie. La taille de la colonie et sa densité peuvent aussi influencer le choix. Le recours saisonnier à la consommation de fourmis n'est relié ni à la disponibilité des nymphes, ni à la qualité des plantes consommées, mais probablement plutôt à la disponibilité d'autres aliments. Les ours ne consomment qu'une fraction des fourmis, 4000–5000, chaque fois qu'ils démolissent un monticule, probablement parce que les fourmis deviennent rapidement difficiles à capturer après l'assaut de la colonie. Les Ours bruns eurasiens consomment plus de fourmis que les ours nord-américains, peut-être à cause de la présence plus fréquente de grandes colonies de fourmis rouges dans les forêts. Il se peut aussi que les fourmis charpentières aient été particulièrement nombreuses au cours de notre étude à la suite d'une importante coupe à blanc.

[Traduit par la Rédaction]

Introduction

Over 180 species of mammals have been recorded eating ants (Hymenoptera: Formicidae) (Redford 1987), including all species of bears, with the understandable exception of the

polar bear (*Ursus maritimus*). One species, the sloth bear (*Melursus ursinus*) of southern Asia, is quite specialized on termites and ants, and use of ants by other bear species appears to decline in generally the following order: American black bear (*Ursus americanus*), brown bear (*Ursus arctos*),

Received July 23, 1998. Accepted December 9, 1998.

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spectacled bear (*Tremarctos ornatus*), sun bear (*Helarctos malayanus*), and Asian black bear (*Ursus thibetanus*) (see the review in Joshi et al. 1997). There is also considerable variation in use of ants among populations within a species (Elgmork and Kaasa 1992; Joshi et al. 1997; Noyce et al. 1997), by season and year within a population (Schwartz and Franzmann 1991; Mattson, et al. 1991a; Clevenger et al. 1992; Joshi et al. 1997; Noyce et al. 1997), and by habitat within an area (Schwartz and Franzmann 1991; Joshi et al. 1997). This variation raises the question of whether ants are a preferred food source that is not always accessible or serve as alternative food when more nutritious foods are not available. There is evidence to suggest that some populations of bears that consume relatively large numbers of ants are not food-stressed. North American black bears in north-central Minnesota consumed more ants than most other black bear populations; this may have been related to the availability of ant species that bears could consume in large quantities (Noyce et al. 1997). These black bears showed a higher rate of body growth than those in other northern locations (Noyce and Garshelis 1998). Brown bears in central Sweden exhibit the highest population growth rate yet recorded for the species (Sæther et al. 1998) and ants contribute about 20% of their annual digestible energy intake (Johansen 1997).

To our knowledge, the seasonal dynamics of bear myrmecophagy in relation to ant availability and species consumed have been studied only in black bears in north-central Minnesota (Noyce et al. 1997). It is important to study the relationship between myrmecophagy, ant ecology, and bear ecology in other areas, both where ants are important as food and where they are not, to identify and understand the factors that affect the exploitation of this potential food source.

We formed the following hypotheses and predictions primarily on the basis of the results obtained by Noyce et al. (1997). In doing this, we assumed that when the myrmecophagous behavior of brown bears in Sweden was similar to that of black bears in Minnesota, a general pattern of bear myrmecophagy was indicated. (i) Bears select among ant species. Noyce et al. (1997) found that black bears selected among ant species. However, most ant-eating mammals likely feed opportunistically and nonselectively (Redford 1987). (ii) Selection of ant species by bears is dependent on the nutrition obtained and efficiency of foraging. Noyce et al. (1997) found that black bears selected species that concentrated densely in nests, whose workers were slow to evacuate the brood when disturbed, and that showed passive defense behavior. Nutritional value, formic acid content, and nest defense and response to attack have been found to influence species selection in other myrmecophagous mammals (Maller and Kare 1967; Redford 1985). (iii) The seasonal consumption of ants by bears is related to the availability of other nutritious foods. This implies that ants are used when other, more nutritious foods are not available. In Minnesota, Noyce et al. (1997) found that the use of ants increased in spring, coincident with increasing abundance of pupae in colonies and decreasing quality of plant foods, specifically increasing dietary fiber content and declining protein levels. Bears shifted from ants to fruits when fruits became widely available in midsummer, despite the continued presence of pupae in nests. (iv) Bears prefer large, densely populated

colonies, but only eat a small portion of the available ants when they excavate a nest; both strategies maximize energy intake per unit handling time. This behavior is common in myrmecophagous mammals (Redford 1985; Noyce et al. 1997).

Study area

The study area encompassed about 13 000 km² in the southern taiga zone of central Sweden, in northern Dalarna County and western Hälsingland (Gävleborg County). Most work was carried out near Noppikoski (61°29'N, 14°51'E). The terrain is hilly; elevations range from 200 to 700 m above sea level but no areas are above treeline. The area consists of productive forest (80%), bogs and lakes (together 20%). The major tree species is Scots pine (*Pinus sylvestris*), which together with the exotic lodgepole pine (*Pinus contorta*) comprises 66% of the forest volume. Other common trees are Norway spruce (*Picea abies*), 32%, and deciduous trees such as common and silver birch (*Betula pubescens* and *Betula pendula*) and aspen (*Populus tremula*), 2%. The forest is intensively managed with clear-cut harvesting, using a harvest rotation of 90–100 years. As a result, 8.4% of the forest area consisted of clearcuts, and 42% was less than 35 years old.

The shrub layer consists of common juniper (*Juniperus communis*), common and silver birch, willows (*Salix* spp.) and mountain ash (*Sorbus aucuparia*). The ground vegetation is a mixture of dwarf shrubs, including bilberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-idaea*), crowberry (*Empetrum* spp.), and heather (*Calluna vulgaris*). The soil surface is mostly covered with mosses and lichens.

The mean temperature in January and July is -7°C and 15°C, respectively. Snow cover lasts approximately 160–170 days from late October until early May, but 2–3 weeks longer in the upper elevations. Precipitation levels and numbers of degree-days in the 150- to 180-day vegetation period (the period with mean temperatures above 5°C) are about 350–450 mm and 800–1100 degree-days, respectively.

Methods

Selection of ant species

We estimated relative consumption by bears of different groups of ants from bear scats collected during 1994–1996. The methods used for analyzing scat contents are described in detail in Dahle et al. (1998). We recorded mass and volume before washing the scats through a 0.8-mm mesh. Five 6-mL subsamples were selected from the residue and analyzed using a 7–30 power stereoscope and a 40–630 power microscope. Here we report frequency of occurrence and fecal volume (estimated visually) of ants by season and year.

To determine the biomass and species of ants available to bears, we inventoried an area of 10 × 10 km around Noppikoski, within the area where scats were collected. Sixty-two randomly chosen points were plotted on a map. Each point marked the northwestern corner of two overlapping sample plots, one 50 × 50 m and one 100 × 200 m. In the smaller plot, all dead wood was opened with an axe. The size of ant colonies within this dead wood, including carpenter ants (*Camponotus herculeanus*), ants in the subgenus *Serviformica* (mostly *Formica fusca* and *Formica lemani*), *Myrmica* spp., *Lasius niger/platythorax*, and *Formica pratensis*, was estimated using regression formulas. These formulas were developed in the same biogeographic region and relate the number of ants seen to the size of colonies (Løken 1993; Rolstad et al. 1998; J. Rolstad and P. Majewski, personal communication). Using this method, only the biomass of wood-dwelling ants that were available to bears was es-

timated, i.e., ants inside live tree trunks and underground roots were not included. All mounds within the large rectangle were counted and their height, width, and length were measured. Numbers of ants in these mounds, including red forest ants, mostly *Formica aquilonia/polycтена*, *Formica exsecta*, and *Formica lugubris*, were estimated on the basis of a regression relating number of ants to aboveground mound volume (Rolstad et al. 1998). Ant biomass was calculated from estimated colony sizes and species-specific ant body masses (Rolstad and Rolstad 1995). This census yielded a rather rough approximation of ant biomass and underestimated numbers of ants in small nests below ground. However, it enabled us to estimate the relative abundance, in terms of total biomass, of carpenter ants and red forest ants.

To document selection of different species of red forest ants, we recorded the frequency of bear excavations of mounds of red forest ants, by species, along established routes. In autumn 1994, we marked and measured (height, width, and length) 201 mounds in six areas near Noppikoski. Each mound was marked with a numbered stick, and classified according to whether or not it had been excavated recently. In 1995, 163 of these mounds were relocated and 4 additional mounds were measured and checked every third week for excavations from June to October. In 1996, 315 mounds in the six areas and three additional areas were visited at 3-week intervals, starting at the end of April. Observations were staggered so that a sample of mounds was checked each week, but each mound was checked only every third week. The species of ants in the mounds were determined from standard reference works (Collingwood 1979; Douwes 1981a, 1981b, 1995). *Formica aquilonia* and *F. polycтена* and *L. niger* and *L. platythorax* were combined into species complexes because they are so difficult to separate.

Factors affecting selection of species

A mixture of pupae and workers of carpenter ants and red forest ants, in similar proportions to those ingested, based on scat analyses, and a sample of pure red forest ant pupae were collected for comparative chemical analyses. We analyzed for formic acid, protein, fat (ether extract), fiber, ash, moisture, and energy contents. The red forest ant sample was a composite of species.

Formic acid content was determined by the Boehringer Mannheim formic acid UV method (Catalog No. 979 732) using a Hewlett Packard 8452A diode spectrophotometer. Nitrogen (N) content was determined using the Kjeldahl method (Association of Official Analytical Chemists (AOAC) 1970). As recommended by Wigglesworth (1972), we subtracted 0.88 from the percentage of N before calculating the crude protein content of workers, to account for N bound in chitin rather than in digestible proteins, but we assumed that the chitin content of pupae was negligible. Fat content was determined by ether extraction, using a Soctec System HT 1043 extraction unit. Dietary fiber was analyzed from enzymatic digestibility using AOAC/NMKL method No. 129 (Nordic Committee on Food Analysis 1989). Ash content was determined by burning the sample at 550°C. Moisture content was determined by drying the samples at 105°C for 16–18 h. Gross energy was determined using a Parr 1271 bomb calorimeter. Digestibility and digestible energy were estimated using these data and regression formulas in Figs. 2 and 3, respectively, in Pritchard and Robbins (1990).

Seasonal use of ants

The seasonal use of ants was determined from scats and the proportion of red forest ant mounds excavated along established routes, described above. Seasons were defined according to the availability of major foods: spring extended from den emergence until 20 May, when the calving season for moose (*Alces alces*) began, summer lasted until 31 July, when berries ripened, and autumn lasted until denning.

To document seasonal availability of ant pupae, 84 mounds of red forest ants were chosen at the beginning of spring 1996 and divided into three groups with similar size ranges. In each season, the mounds in one group were excavated down to mineral soil. The contents were frozen to kill the ants, then weighed. Subsamples composed of at least 50% of this material were taken, from which pupae were extracted and weighed to the nearest gram and the total biomass of pupae in the mound was estimated.

Foraging behavior

It was not possible to observe foraging behavior directly, so we tracked six radio-marked bears when snow cover was present in spring, at a time when they actively foraged on red forest ants. We used data from bears followed continuously far enough that they produced at least 4 scats. For the six bears, this was a total tracked distance of 60 km and represented about 14 days of bear activity. We counted excavated mounds, gathered scats, and estimated the amount of ants ingested, using the estimated volume of ants in each scat and a correction factor of 1.1 to correct fecal matter to ingested matter (Hewitt and Robbins 1996; Dahle et al. 1998). From this, we calculated the mass of ants consumed for each excavated mound. This method assumes that the foraging behavior of bears was relatively constant, being similar before they were tracked and during the tracking period. On the basis of following tracks on spring snow for a total of 640 km for various studies, we believe that this is a reasonable assumption.

Results

Selection of ant species

Of the 62 plots chosen for the ant census, 7 were in nature reserves or located in water and could not be included in the study. Of the remaining 55 plots, 50 contained ants. Density averaged 3.8 ant colonies/ha (SE = 0.43 colonies/ha) for the 55 plots. The estimated ant biomass available to bears was 9.4 kg/ha for ants in mounds, mostly red forest ant species, and 0.2 kg/ha for wood-dwelling species, for a total of 9.6 kg/ha (Table 1).

Ants occurred in 61, 78, and 25% of the scats in spring, summer, and autumn, respectively (Table 2). Red forest ants and carpenter ants predominated in the scat samples. Red forest ants were found more frequently and in larger volumes than carpenter ants in spring, but declined sharply in volume until summer, and declined further in frequency and volume until autumn. Carpenter ants predominated in summer (Table 2). The only other ants identified in the scats were *Myrmica* spp., and *Serviformica* workers, but they were relatively unimportant on a volume basis (Table 2).

Only red forest ants were consumed in greater quantities than carpenter ants, and then only in spring (Table 3). The ratio of red forest ant volume to carpenter ant volume in scats was 10:1 in spring, 0.5:1 in the summer, and 0.3:1 in autumn. Relative to availability, carpenter ants were consumed more than other groups in all seasons (Table 3).

Use of red forest ant species was documented by comparing the species of ants in excavated mounds with those available in the mound-excavation study (Table 4). When data from all 3 years were combined, we found a significant difference in proportions of mounds excavated among the three most common species ($\chi^2 = 10.48$, $df = 3$, $P = 0.005$). *Formica aquilonia/polycтена* showed the highest selection index for all years combined, whereas *F. exsecta* and

Table 1. Estimated dry biomass of ants available to bears, by group, in the study area, based on 55 study plots.

Ant group or species	Dry mass (g/ha)		Biomass (g dry mass/100 individuals) ^a
	Mean	SE	
Red forest ants ^b	9400	1080	0.28
Subgenus <i>Serviformica</i> ^c	106	26.3	0.17
<i>Myrmica</i> spp. ^c	56	10.6	0.17
Carpenter ants ^d	23	7.9	1.24
<i>Formica pratensis</i> ^c	18	8.4	0.36
<i>Lasius niger/platythorax</i> ^c	0.005	0.005	0.10
Total	9600	1133	

^aFrom Rolstad and Rolstad (1995) and P. Majewski (personal communication).

^bMound-living.

^cLiving in dead wood and earth.

^dLiving in dead and live wood.

Table 2. Frequency of occurrence (FO) and percent volume (V) of ants in brown bear scats by season (data from 1994–1996 combined).

Ant group	Spring (N = 139)		Summer (N = 83)		Autumn (N = 132)	
	FO	V	FO	V	FO	V
Red forest ants						
Workers	56	10	56	5	15	1
Pupae	1	—	7	—	3	—
Carpenter ants						
Workers	10	1	48	10	20	2
Pupae	0	—	6	—	4	1
<i>Myrmica</i> spp., workers	6	—	20	1	1	—
<i>Serviformica</i> , workers	4	—	7	—	2	—
Unidentified workers	0	—	0	—	1	—
Combined	61	12	78	16	25	4

Note: A dash denotes a trace (<0.5%).

F. lugubris appeared to be used less than expected (Table 4). We also tested the frequency of excavation for each year separately. No differences in frequency of excavation were found among species in 1994 ($\chi^2 = 2.32$, $df = 2$, $P = 0.31$) or 1995 ($\chi^2 = 0.77$, $df = 2$, $P = 0.68$). In 1996, however, there was a marginally significant difference ($\chi^2 = 5.64$, $df = 2$, $P = 0.06$), with a somewhat higher frequency of excavation of *F. aquilonia/polyctena* mounds. A comparison of the frequency of excavation of *F. aquilonia/polyctena* mounds with that of all other species' mounds combined in 1996 showed a statistically significant difference ($\chi^2_c = 5.03$, $df = 1$, $P = 0.02$).

There was a significant difference in the volume of mounds among species (ANOVA, $F_{[3,158]} = 4.99$, $P = 0.002$). A Fisher's protected least significant difference test revealed that the mounds of *F. aquilonia/polyctena* were significantly larger than those of the other species. In 1995, the excavated mounds were longer (Mann–Whitney test, $U = 2469.5$, $N = 167$, $P = 0.03$) and wider ($U = 2508.5$, $P = 0.04$) than the unused mounds. Also, mounds that had been excavated more than once during 1995 had a greater volume ($U = 47$, $N = 56$, $P = 0.02$) than mounds that had been excavated only once. In 1996, no mounds were excavated more than once.

The bears excavated the same mounds more than expected in both 1994 and 1995. In 1994, 48 of the 167 mounds were excavated and in 1995, 23 of these were excavated again ($\chi^2 = 6.25$, $df = 1$, $P = 0.02$).

Factors affecting selection of species

Carpenter ants contained 71% more fat than red forest ants, one-fourth as much formic acid, and about one-half the dietary fiber; this contributed to its higher predicted digestibility (Table 5). Red forest ant pupae had a high fat content, but also a high fiber content and did not provide bears with more digestible energy than red forest ant workers (Table 5).

Carpenter ants were much larger than other ants in the study area (Table 1). They were also slower to attack when their nests were opened, and they evacuated the pupae more slowly.

Seasonal and annual use of ants

Percent volume of both carpenter and red forest ants in spring scats varied among the 3 years of the study, but no statistical differences were found among years in summer and autumn scats (Table 6). Red forest ants composed a significantly lower volume of scats in spring in 1996 than in both 1994 ($U = 752.5$, $df = 1$, $P < 0.001$) and 1995 ($U = 1433.0$, $df = 1$, $P < 0.01$). Bears ate significantly more carpenter ants in spring in 1994 than in 1995 ($U = 586.0$, $df = 1$, $P < 0.001$) and 1996 ($U = 625.0$, $df = 1$, $P = 0.007$).

The proportion of mounds of red forest ants that were excavated also varied significantly among years ($\chi^2 = 51.2$, $df = 2$, $P = 0.001$): 29, 33, and 8% in 1994, 1995, and 1996, respectively (Table 7). This difference was influenced by the inclusion of new mounds in the 1996 sample, because the new mounds were excavated less often (1%) than the continuously monitored mounds (14%, $\chi^2_c = 19.9$, $df = 1$, $P < 0.0001$). Nevertheless, there was still significant variation in the proportions of mounds excavated during the 3 years when only mounds monitored in all years were included ($\chi^2 = 18.0$, $df = 2$, $P < 0.0001$). Mounds were excavated less in 1996 than in either 1994 ($\chi^2_c = 10.3$, $df = 1$, $P = 0.001$) or 1995 ($\chi^2_c = 16.7$, $df = 1$, $P < 0.0001$).

In both 1995 and 1996, when excavation activity was recorded for all seasons, there was significant seasonal varia-

Table 3. Relative use of ant groups by bears, based on scat analyses, and relative abundance of ants in the study area, based on biomass estimates.

Ant group	Total biomass in area	Relative frequency in scats			Relative volume in scats		
		Spring	Summer	Autumn	Spring	Summer	Autumn
Red forest ants	409	5.6	1.2	0.8	10	0.5	0.3
<i>Serviformica</i>	4.6	0.4	0.1	0.1	—	—	—
<i>Myrmica</i> spp.	2.4	0.6	0.4	0.1	—	0.1	—
Carpenter ants	1	1	1	1	1	1	1

Note: The results are scaled so that carpenter ants equal 1. A dash denotes <0.05.

Table 4. Percentages of mounds excavated by brown bears along the transect routes, according to red forest ant species, 1994–1996.

Ant species	1994	1995	1996	Selection index ^a
<i>F. aquilonia/polyctena</i>	32 (135)	35 (135)	10 (212)	+0.13
<i>F. lugubris</i>	25 (16)	25 (16)	0 (36)	-0.54
<i>F. exsecta</i>	10 (10)	40 (10)	4 (53)	-0.75
<i>F. pratensis</i>	— (0)	— (0)	0 (9)	—
<i>Formica truncorum</i>	— (0)	— (0)	0 (1)	—

Note: Numbers in parentheses are sample sizes.

^aCalculated as $\ln(\Sigma \text{ observed values} / \Sigma \text{ expected values from the } \chi^2 \text{ test})$; positive index values indicate more use than expected.

Table 5. Analysis of nutrient composition, gross energy, and digestibility of the most important ant groups used as food by brown bears in the study area in south-central Sweden (summer samples).

	<i>Camponotus herculeanus</i> ^a	<i>Formica</i> spp. ^b	<i>Formica</i> spp., pupae
Dry matter ^c (%)	31.2	26.7	24.4
Protein ^c (%)	43.8 ^d	55.9 ^d	54.9 ^e
Dietary fiber ^c (%)	9.3	17.4	26.6
Ash ^c (%)	4	5	4
Fat ^c (%)	19.4	11.3	18.4
Formic acid ^f (%)	2.3	8.4	Not measured
Dry matter digestibility ^f (%)	88.4	77.1	64.3
Gross energy ^g (kJ/g)	21.9	20.8	23.7
Digestible energy ^h (kJ/g)	20.6	17.7	17.8

^aSample consisted of about 80% workers and 20% pupae, to mimic intake by bears.

^bSample consisted of about 90% workers and 10% pupae, to mimic intake by bears.

^cAnalyzed by the Norwegian Institute for Nutritional Research, Ås.

^dProtein content was calculated as $(\%N - 0.88) \times 6.25$ to correct for the protein bound in chitin (following Noyce et al. 1997).

^eProtein content was calculated as $\%N \times 6.25$, assuming no protein bound in chitin (Noyce et al. 1997).

^fCalculated from the equation given in Fig. 2 in Pritchard and Robbins (1990).

^gAnalyzed by Akvaforsk, Sunndalsøra, Norway.

^hCalculated from the equation in Fig. 3 in Pritchard and Robbins (1990).

tion in excavation activity ($\chi^2 = 9.1$, $df = 2$, $P = 0.001$, and $\chi^2 = 13.3$, $df = 2$, $P < 0.001$, respectively). In both years, the lowest activity rate was observed in autumn. The rate of excavation of mounds of red forest ants, recorded by week, declined significantly from late May to the end of July in 1995, based on 547 observations of 167 mounds (logistic regression, $\chi^2 = 6.14$, $df = 1$, $P = 0.013$).

The proportion of mounds with pupae was 27% in spring, 68% in summer, and 46% in autumn 1996 (Table 8). This difference was significant ($\chi^2 = 9.1$, $df = 2$, $P = 0.01$). The total mass of pupae in the mounds also varied among sea-

sons, the highest value also being reached in summer (Kruskal–Wallis analysis of variance, corrected for ties, $H = 12.5$, $df = 2$, $P = 0.002$; Table 8).

Foraging behavior

Six bears were followed continuously on the snow in spring long enough to obtain a minimum of 4 scats from each bear; the total tracked distance of 60 km represented about 14 days of bear activity. The mean mass of red forest ants consumed per excavated mound was relatively constant, 47.5 ± 2.6 (SE) g wet mass (Table 9), or 13 ± 0.7 g dry

Table 6. Percent volume of remains of the two major ant groups, carpenter ants (CA) and red forest ants (RFA), in brown bear scats by season and year.

Year	Spring			Summer			Autumn		
	CA	RFA	N	CA	RFA	N	CA	RFA	N
1994	4	9	29	7	5	35	3	1	44
1995	0	21	56	14	4	30	2	—	58
1996	—	1	54	9	7	18	4	2	30

Note: A dash denotes a trace (<0.5%).

mass, based on percent dry matter from Table 5. Using the mass of individual ants (Table 1), this corresponds to about 4000–5000 ants (4600 ± 500 , 95% confidence interval) per excavated mound.

Discussion

Relative importance of ants to brown bears in central Scandinavia

Ants were an important food source for brown bears in this area, especially in spring and summer, providing an estimated 20% of the total annual digestible energy (Johansen 1997). In addition, 23% of the mounds of red forest ants in the study area, on average, were excavated annually.

The amount of ant biomass available on the forested land in the study area was estimated to be 9.6 kg/ha, which represents 7.7 kg/ha over the entire area, after lakes and bogs are accounted for. The estimated density of the bear population in our study area was 20–25 bears/1000 km² (J.E. Swenson and F. Sandegren, unpublished data). Therefore, the amount of available ant biomass was about 30.5–38.5 tonnes for each bear. For comparison, the amount of the other important prey for this bear population, moose, that was available was about 30% of that value, 3.1 kg/ha over the entire area in winter (based on winter aerial censusing; G. Cederlund, personal communication). Sweden has high moose densities compared with most other parts of the geographical range of moose (Cederlund and Bergström 1996), so in most areas of the boreal forest, the ratio of ant biomass to moose biomass would be even higher.

Selection of ant species

Noyce et al. (1997) suggested that in a given location, North American black bears preferred ant species that provided the most efficient foraging with the least discomfort from ants that attacked or tasted bad, by virtue of their nest size, density of workers, nutritional content, and defensive behavior. Based on the results of Noyce et al. (1997), we hypothesized that brown bears select ant groups in the following order: (i) carpenter ants, (ii) red forest ants, and (iii) other ants. Our results support this hypothesis. Carpenter ants were strongly selected compared with red forest ants, and selection of carpenter ants increased during the year. Moreover, carpenter ants are more difficult to obtain because they live in smaller colonies and in dead wood. Thus, carpenter ants are highly preferred. Ant species in the genus *Camponotus* appear to be most frequently preyed upon by myrmecophagous mammals generally (Redford 1987), probably in part because *Camponotus* is one of the

Table 7. Percentages of red forest ant mounds excavated seasonally by brown bears, 1994–1996.

	1996		Monitored in all years	All mounds
	1994	1995		
Spring	—	23 (43)	9 (167)	5 (315)
Summer	—	21 (167)	5 (167)	3 (315)
Autumn	—	8 (167)	0 (167)	0 (315)
Combined	29 (167)	33 (167)	14 (167)	8 (315)

Note: For 1996 the sample is separated into mounds that were also monitored in 1994 and 1995 and the entire sample, including the mounds added for monitoring in 1996. Numbers in parentheses are sample sizes.

Table 8. Biomass of red forest ant pupae in mounds excavated in different seasons in 1996.

	No. of mounds	Biomass (g)		Mounds with pupae (%)
		Mean \pm SE	Max.	
Spring	28	18.3 \pm 9.1	237	27
Summer	28	59.0 \pm 14.2	299	32
Autumn	28	13.3 \pm 5.9	124	46

Table 9. Wet and dry mass of red forest ants obtained per excavated mound by six brown bears followed continuously on the snow in the spring.

Bear No.	No. of scats	No. of excavated mounds	Ant volume (mL)	Mean mass per mound (g)	
				Wet	Dry
9102	5	36	387	48	12
9306	7	15	146	40	11
9402	4	20	194	40	11
8906	4	9	102	46	12
9503	5	7	102	59	16
9609	4	28	369	53	15

three most species-rich ant genera in the world (Wilson 1976). But carpenter ants are commonly eaten by both brown/grizzly bears and black bears in North America, even in areas where other ant species are more common (see the review in Noyce et al. 1997).

Two other groups of ants that often inhabited dead wood, *Myrmica* spp. and the subgenus *Serviformica*, were more common than carpenter ants, but were eaten by bears to a smaller degree in relation to their abundance than carpenter ants in every season. Johnson (1996) and Noyce et al. (1997) also found that black bears ate few *Myrmica* spp., and Onoyama (1988) reported that brown bears ate fewer ants of the family Myrmecinae, which includes *Myrmica* spp., than expected.

Grimal'skii (1975) and Atanassov (1983) implied, but did not show statistically, that European brown bears selected among *Formica* species. We found a significantly higher frequency of excavation of *F. aquilonia/polycytena* mounds than

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are relatively few studies reported of the food habits of brown bears in the North American boreal forest (McLellan and Hovey 1995).

Bears excavated 8–31% of the mounds of red forest ants in our study area annually. Relatively high proportions of excavated mounds have been reported from many areas in Europe. In Russia, bears excavated 93% of 87 examined mounds in the Sayan Mountains (Boltunov 1993), 50% of the mounds in the Onezhsky Peninsula (Vaisfeld 1993), 32–37% of *Formica* spp. mounds in the Ural Mountains (Rubinshtein 1976), 22% of *Formica* spp. mounds and 5.5% of those of smaller ants (*Lasius* spp. and *Myrmica* spp.) in the Volga–Kama Region (Loskutov and Radchenko 1991). In Belarus, bears excavated 60% of the mounds of *F. polyctena* (Grimal'skii 1975). Atanassov (1983) reported the following proportions of excavated mounds from five areas in Bulgaria: 9–18% for *F. lugubris*, 9–11% for *F. rufa*, 4% for *F. pratensis*, and 0–2% for *F. exsecta*. Elgmork and Unander (1998) reported that bears in Norway excavated and foraged from 38% of the mounds within 15 m of their tracks on spring snow (44% in total when those excavated for other purposes are included). We have found no comparable records of mound excavation by brown bears in North America.

Eurasian brown bears in the boreal forest may feed on mound-building ants more than North American brown bears because of availability. The Eurasian taiga seems to offer optimum habitats for forests ants that build large mounds (Savolainen et al. 1989). An average mound in our study area had a height of 61 cm and diameter of 81 cm; maximum measurements were 1.40 and 2.34 m, respectively. In southern Finland, 60% of the mounds of red forest ants were less than 50 L in aboveground volume, 25% were 50–300 L, and 15% were over 300 L, with a few over 2000 L (Vepsäläinen and Wuoreninne 1978). We found a colony density of about 3.8/ha, most of which was represented by red forest ants. This density is similar to that found in the southern half of Finland (Rosengren et al. 1979) and southern Norway (Elgmork and Unander 1998), and is about 100 times the densities commonly reported from Central Europe (Rosengren et al. 1979). These are average densities, but colonies are clumped. Savolainen et al. (1989) reviewed the literature and reported local densities of 130–180 mounds/ha in Palearctic boreal forests. Palearctic species of red forest ants often build large mounds (1–2 m high), representing a considerable concentration of ants. Nest densities can also be high in the Nearctic region (Savolainen et al. 1989; Noyce et al. 1997), but nests are considerably smaller (Elgmork and Kaasa 1989) or are mostly ground nests, not mounds. The North American black bears studied by Johnson (1996) and Noyce et al. (1997) dug out ground nests of ants.

In the case of carpenter ants, there are probably more similarities between those in the Palearctic and Nearctic boreal forests. They are among the most common and widespread ants there, several species dominate ant communities (Sanders 1970; Punttila et al. 1991), and the species seem to differ little in their biology (Sanders 1964). They are most abundant in mature forests, where they live in dead trees and logs, and some species inhabit large live trees (Sanders 1970; Punttila et al. 1991). However, carpenter ants rapidly colonize dead wood and stumps after clear-cutting (Sanders 1970), consequently the carpenter ant biomass available to bears is highest

in young stands, 5–30 years following clear-cutting (Rolstad et al. 1998). Almost 30% of our study area was forest 5–35 years following clear-cutting, which suggests that the available biomass of carpenter ants may have been relatively higher than that in managed boreal forest with fewer clearcuts. Schwartz and Franzmann (1991) reported that North American black bears which lived in an old burn fed more on carpenter ants than those in a younger burn because they were able to open the more rotted logs in the older burn.

In conclusion, ants represent an enormous potential food resource for bears in the boreal forest. The degree to which this resource is exploited probably depends on the availability of these ants in relation to the abundance and availability of other nutritious food. Even if ants are rarely used, they are potentially an important food source if other sources fail. It would be useful to document the abundance and availability of ants in an area where bears do not regularly use ants, in order to clarify this relationship. Also, one test of this hypothesis would be to compare the food habits of brown bears along a north–south gradient in the boreal forest. If the level of predation on ungulates in spring declines from north to south, as was reported by Danilov (1983), we predict that the use of ants will be found to increase from north to south with declining use of ungulates.

Acknowledgments

We thank Thomas Johansen, Bjørn Dahle, and Andreas Norin for helping us with the fieldwork, Matti Naukkarinen for identifying the ants, Przemyslaw Majewski for introducing us to census methods for ants, Sven Brunberg for assistance in Noppikoski, and Orsa Besparingskog for providing a place for us to live during the field seasons. Karen Noyce, Thomas Johansen, Bjørn Dahle, Ole Opseth, Jørund Rolstad, Ole Jakob Sørensen, Göran Englund, and John Linnell made helpful comments on the manuscript. The chemical analyses were conducted at the Norwegian Institute for Nutritional Research, Ås, except for the determination of gross energy, which was done at Akvaforsk, Sunndalsøra, Norway. This study was financed by the Swedish Hunters' Association, the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the Norwegian Institute for Nature Research, and World Wildlife Fund Sweden. This study was part of the Scandinavian Brown Bear Research Project.

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the study area consumed an estimated 6.5 moose calves during its first 4 weeks of life, primarily in June (Busk 1998).⁴ We suggest that the availability of other nutritious foods is the major factor influencing the use of ants by bears, as was concluded by others for bears foraging on ants (Schwartz and Franzmann 1991; Noyce et al. 1997) and army cutworm moths (*Euxoa auxiliaris*) (Mattson et al. 1991b). This suggests that ants, especially red forest ants, represented a secondary food source, used primarily when other foods were less available. Clevenger et al. (1992) found that ants (species not identified) were not an important food of brown bears in Spain, except when snow in spring was >10–12 cm deep, covering other potential food sources; then they fed heavily on ants. Also, Mattson et al. (1991a) reported that grizzly bears in the Yellowstone area only used ants heavily in 1 of 11 years.

In the autumn, when berries are abundant, ants were used the least, as expected. Where energy-dense foods are not available, berries are essential for bears to provide energy reserves necessary for reproduction and winter hibernation (Welch et al. 1997).

The relatively lower use of carpenter ants in spring may reflect their availability. Hölldobler and Wilson (1990) reviewed and compared the early spring behavior of *F. polyctena* and *C. herculeanus*. *Formica polyctena* are able to raise the internal mound temperature rapidly during early spring, owing to metabolic heat production combined with the physical properties of the mound that enhance collection of heat from the sun. *Camponotus herculeanus* does not show these adaptations, is dependent on ambient temperature, and therefore becomes active much later in the spring. Carpenter ants also overwinter in large trees and underground in roots, where they are inaccessible to bears (Hölldobler and Wilson 1990). Thus, it is not surprising that carpenter ants were not found in bear scats collected in spring 1995, which was the coldest and latest spring during the study.

Consumption patterns when ant colonies are attacked

Noyce et al. (1997) found that North American black bears tended to feed briefly at many colonies, often leaving many ants uneaten, perhaps to maximize energy intake per unit handling time. This has been recorded for many other myrmecophagous mammals, and is probably a response to the rapid increase in difficulty of capturing prey after a colony is attacked (Redford 1985).

We were able to document that bears took a quite stable and relatively small number of ants, 4000–5000, each time they opened a mound of red forest ants in the spring. This is a small proportion of the ants available, e.g., *F. polyctena* colonies have 100 000 – 1 million workers (Savolainen and Vepsäläinen 1988), with extremely large colonies numbering up to 3 million workers (Gößwald 1989). Foraging on red forest ants may be more efficient in the spring than in other seasons. Ants move more slowly when it is cold, and often concentrate at the top of the mound, where they are warmed by the sun. Elgmork and Unander (1998) reported a mean excavation depth into the mound of 24 cm in spring, the mean height of the mound being 94 cm. This suggests that

they “skimmed off” the top of the mound, where the density of ants was greatest. However, the greater use of available carpenter ants than of available red forest ants suggests that the bears consume a much larger proportion of the available ants when they open a carpenter ant mound than when they excavate a red forest ant mound. This apparently greater use of available carpenter ants is consistent with the hypothesis that bears maximize energy intake per unit handling time. It was more time- and energy-consuming to break into a carpenter ant colony in dead wood than to excavate a mound of red forest ants, but the carpenter ants were slower to respond aggressively and evacuate pupae.

Why do bears eat ants, or why do some bear populations not eat many ants?

Ants provided an abundant, stable, and predictable food resource, rich in both protein and energy, for the bears in central Sweden, even when other foods were scarce. That the bears utilized this resource intensively and extensively is evident from the estimate that 20% of the annual digestible energy intake of bears on our study area came from ants (Johansen 1997). Also, about one-fourth of the mounds of red forest ants were excavated annually, and carpenter ants were exploited to a much greater degree. Not only can ants be an important source of protein and energy, but they may also provide essential amino acids that are unavailable in other spring foods (Eagle and Pelton 1981; Redford and Dorea 1984; Noyce et al. 1997). The study of Noyce et al. (1997) and our study show how ants are important for two productive bear populations. This is not a universal situation, however. Schwartz and Franzmann (1991) compared two black bear populations in Alaska and found a higher rate of body growth in the population that fed less on ants but more on moose calves.

Ants are an important component of the diet of brown bears in many areas of Eurasia, such as southern Norway (Elgmork et al. 1978; Elgmork and Kaasa 1992), north-central Scandinavia (Dahle et al. 1998), Belarus (Grimal'skii 1975; Lavov 1993), Bulgaria (Atanassov 1983), the Ukraine (Slobodyan 1993), south of the Ural Mountains (Loskutov and Radchenko 1991), northwest of the Ural Mountains (Vaisfeld 1993), the western Sayan Mountains (Boltunov 1993), Kazakhstan (Baidavletov 1993), central Siberia (Zavatskii 1978), and Hokkaido Island, Japan (Onoyama 1988). However, this does not seem to be the case in North America. The fecal volume of ants in spring, summer, and autumn in our study area was 12, 16, and 4%, respectively, and in the Sayan Mountains in southern Russia was 7.6% on an annual basis (Boltunov 1993). In studies of grizzly bears, fecal volumes were 2.8, 5.3, and 4.3% in Yellowstone National Park and 0.2, 2.3 and 1.5% in British Columbia in spring, summer, and autumn, respectively (Mattson et al. 1991a; McLellan and Hovey 1995). This is consistent with the review of Elgmork and Kaasa (1992), which showed that the Formicidae constituted one of the main food sources (in spring) of brown bears in 6 of 18 studies carried out in Eurasia, particularly north of a latitude of about 55°N, but in none of the 9 studies from North America. However, there

⁴H. Busk. 1998. Brown bear (*Ursus arctos*) predation on moose (*Alces alces*) calves in a Swedish boreal forest. Undergraduate thesis, Swedish University of Agricultural Science, Uppsala.

those of other *Formica* species. However, when analyzed by year only, the difference was significant only in 1996, when the use of ants was lowest. *Formica aquilonia/polycтена* had the largest mounds, and larger mounds were preferred. For all years combined, only *F. aquilonia/polycтена* mounds were excavated more than expected; *F. lugubris* and *F. exsecta* mounds were excavated less than expected on the basis of availability.

Our results are consistent with the European literature, which shows that brown bears generally prefer *F. polycтена* and avoid *F. exsecta*. Grimal'skii (1975) reported that brown bears in Belarus preferred *F. polycтена* over *Formica rufa* and avoided *F. exsecta*. Elgmork and Kaasa (1992) found that brown bears in southern Norway ate primarily *F. aquilonia/polycтена*; *F. fusca* was less important and *F. exsecta* and *Formica sanguinea* occurred only sporadically. Carpenter ants were apparently not commonly eaten. Those authors did not document availability. Atanassov (1983) recorded a higher frequency of excavation of *F. lugubris* and *F. rufa* mounds and a lower frequency for *F. exsecta* and *F. pratensis* mounds.

We cannot explain the reduction in excavation activity in our study areas in 1996 compared with 1994 and 1995. It is, however, a reflection of reduced foraging on red forest ants, as fewer red forest ants were found in the bear feces analyzed in 1996 than in 1994 and 1995, at least in spring.

Factors involved in selection of ant species

Based on the results of Maller and Kare (1967), Redford (1985), Johnson (1996), and Noyce et al. (1997), we predicted that bears selected ants that occurred in dense colonies, had a low formic acid content, were slower to evacuate pupae from a disturbed nest, and were less aggressive in defending the nest. Our results support many of these predictions, although it is difficult to determine specifically which characteristics the bears used to select species, because these characteristics are species-specific. The chemical analyses showed that carpenter ants contained less formic acid than red forest ants, in addition to having a higher fat content and less dietary fiber, which contributed to the higher digestibility. In addition, carpenter ants were slower to evacuate pupae from disturbed nests, slower to disperse, perhaps because they were more confined in the wood, and less aggressive in defending the nest than red forest ants. Carpenter ant colonies were relatively small, ca. 100–1000 workers (Savolainen and Vepsäläinen 1988). Red forest ants contained a higher amount of protein than carpenter ants.

Among the red forest ants, the species with the largest mounds, *F. aquilonia/polycтена*, was the most preferred by brown bears, as Grimal'skii (1975) also reported from Belarus. Savolainen and Vepsäläinen (1988) found that the colonies of *F. polycтена* were at least two orders of magnitude larger than those of other common ant species in southwestern Finland.

Noyce et al. (1997) also predicted that bears selected ant species according to body size. Carpenter ants were the largest ants available in our study areas (Table 1). However, the black bears studied by Noyce et al. (1997) preferred small ants. Also, their prediction that bears select ants with larger body sizes might be circular, because they referred to the lit-

erature when predicting that bears would prefer carpenter ants elsewhere, and carpenter ants are large.

The ant species most preferred by brown bears exhibited the following characteristics: low formic acid content, high digestible energy, and less aggressive defense behavior and slower dispersal when the colony was disturbed. Giant ant-eaters (*Myrmecophaga tridactyla*) apparently also chose termite species according to their nutritional value, mound defense, and response to attack (Redford 1985). The importance of formic acid is supported by the finding that captive armadillos (*Dasyus novemcinctus*) reduced their food intake when formic acid was added to the food (Maller and Kare 1967). The influence of the body size of ants is unclear; carpenter ants might have been selected because of factors other than their size.

Factors involved in the seasonal pattern of ant use

Noyce et al. (1997) found that the seasonal use of ants increased coincidentally with a rise in the number of pupae in nests, but also with a decrease in the quality of spring food. Thus, those authors were unable to discern which, if either, was the more important influence. They concluded that the presence of pupae alone seemed to be insufficient to explain the seasonal pattern of use, because the most preferred species in their area had the fewest visible pupae per opened nest, and feeding on ants declined when fruits ripened, despite the continued presence of pupae in nests.

In this study, the use of mounds decreased from spring to autumn. This did not correspond to the availability of pupae, which were most abundant in summer. Thus, the presence of pupae cannot be the major factor influencing excavation of mounds by brown bears in our study area. This conclusion is also supported by the findings that pupae did not provide more digestible energy than *Formica* spp. workers and that pupae constituted a smaller portion of the diet than workers. Also, Johnson (1996) found no selection of ant colonies with pupae by two wild but human-habituated North American black bears.

We did not measure levels of total dietary fiber and protein in the plant food of bears. However, it has been documented that fiber levels increase and protein levels decline in plants during the growing season (Albon and Langvatn 1992; McLellan and Hovey 1995; Noyce et al. 1997). Therefore, if the nutritional quality of plant foods was influencing the use of ants, we would expect to see an increasing trend towards the use of ants, measured by excavation of mounds of red forest ants, during the plant growing season, from green-up to the appearance of fruits of Ericaceae. We did not find the expected increase in use of ants during this period; in fact, there was a significant decline. The seasonal presence and weekly use of carpenter ants were not documented in our study.

The seasonal use of ants is probably best explained by the seasonal availability of other foods, which is of course a local phenomenon. In our study, the quality of herbaceous vegetation and ant pupae did not correlate with ant consumption. While the quality of herbaceous vegetation may have been an important factor in Minnesota (Noyce et al. 1997), moose calves were a more important summer food in our study area (Johansen 1997). Each bear >2 years old in

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