Black bears as ant-eaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota

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Abstract: We documented the seasonal occurrence and volume of different ant species in black bear (*Ursus americanus*) scats in north-central Minnesota. We determined nest densities of common ant species in strip transects and compared their use by bears with their availability. We recorded phenologic change in ant-nest characteristics and measured the nutritional composition of ant workers, ant pupae, and herbaceous spring foods of bears. Consumption of ants was higher than reported elsewhere, peaking in early July, when ants constituted 58% of scat volume and occurred in 96% of scats. Increased consumption of ants in late spring coincided with (*i*) increased abundance and size of ant brood in nests and (*ii*) decreased protein and increased fiber levels in herbaceous foods. *Lasius umbratus* was the principal species consumed at 1 site, whereas *L. umbratus*, *Acanthomyops interjectus*, and *A. claviger* dominated the diet farther south. These ants were likely preferred to other equally abundant species because of their sometimes dense concentrations inside nests, passive behavior, and distinctive odor, enabling bears to forage more efficiently than on other species. We suspect that regional differences in ant consumption are due to differences in local availability of these species. Where they are less common, bears likely select large-bodied ants, usually *Camponotus* and *Formica* species.

Résumé : Nous avons étudié la présence saisonnière et le volume de différentes espèces de fourmis présentes dans les fèces d'Ours noirs (*Ursus americanus*) dans le centre nord du Minnesota. Nous avons déterminé la densité des fourmilières des espèces communes le long de transects en bandes et comparé leur exploitation par les ours à leur disponibilité. Nous avons étudié la phénologie des caractéristiques des fourmilières et mesuré la valeur nutritive des ouvrières, des nymphes et des plantes herbacées mangées par les ours au printemps. La consommation des fourmis s'est avérée plus élevée que partout ailleurs et maximale au début de juillet, et les fourmis constituaient 58% des fèces (en volume) et ont été retrouvées dans 96% d'entre elles. L'augmentation de la consommation de fourmis au printemps coincidait avec (*i*) l'augmentation de l'abondance et de la taille de la progéniture des fourmis dans les nids, (*ii*) la diminution des protéines et l'augmentation des fibres dans les plantes herbacées. *Lasius umbratus* constituait la principale espèce consommée à 1 site, alors que *L. umbratus*, *Acanthomyops interjectus* et *A. claviger* dominaient dans le régime plus au sud. Ces fourmis étaient probablement préférées à d'autres espèces tout aussi abondantes à cause de leur densité à l'intérieur des fourmilières, leur comportement passif et leur odeur distinctive, ce qui rendait leur détection plus facile pour les ours. Nous croyons que les différences régionales dans la consommation des fourmis sont dues à la disponibilité ponctuelle de ces espèces. Là où elles sont moins abondantes, les ours choisissent probablement des fourmis plus grosses, généralement des espèces de *Camponotus* et *Formica*.
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Introduction

Insects are a common component in the diet of North American black bears (*Ursus americanus*), with ants (Hymenoptera: Formicidae) predominating in most locations (Hatler 1972; Beeman and Pelton 1980; Grenfell and Brody 1983;

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Raine and Kansas 1990; Schwartz and Franzmann 1991). Black bears display several traits characteristic of large specialized mammalian myrmecophages (Redford 1987), including forelimbs suitable for digging or penetrating nests, long agile tongues for extracting insects quickly and with minimal ingestion of debris, and use of smell to help locate nests. However, ants generally constitute only a small proportion of the diets of black bears, leading to speculation that they serve primarily as a source of specific nutrients otherwise lacking in bear diets (Eagle and Pelton 1981; Redford 1987; McDonald and Fuller 1994) rather than as a significant source of calories.

Omnivory has likely limited the degree to which black bears are specialized for ant-feeding; bear species that feed more exclusively on colonial insects (e.g., sloth bears (*Melursus ursinus*) and sun bears (*Helarctos malayanus*)) have longer, more agile tongues, as do other specialized myrmecophages. Whereas vermilinguas consume <1% debris when eating termites (Montgomery 1985*a*), black

bears often ingest nest material when feeding on ants. Evolutionary pressures against morphologic specialization in black bears may, however, have favored behaviors or prey preferences that maximize nutritional returns from hunting these tiny prey.

Preliminary observations indicated that ants were more prevalent in the scats of black bears in north-central Minnesota than elsewhere and that their occurrence as a major dietary component was distinctly seasonal, spanning about 6–8 weeks in June and July (Garshelis et al. 1988). Ants appeared to be available to bears throughout the spring and summer, however, prompting us to hypothesize that phenologic changes in ant colonies (population size, composition, etc.) were influencing the attractiveness of ants to bears as prey. Alternatively, changes in spring plant foods as they matured might also be altering bears' food preferences. Whatever the cause, it was clear that bears were not simply consuming ants opportunistically but were being selective, at least with regards to *when* to eat ants. We hypothesized that bears might also be choosing which ants to eat, particularly if some species offered greater nutritional return per unit foraging effort than others.

To test these hypotheses, we measured the seasonal occurrence of ants in bear scats and tracked seasonal changes in several characteristics of ant nests. We compared the species-specific composition of scats with ant availability and performed nutritional analyses on ants and several plants commonly eaten by bears.

Study area

We conducted most fieldwork (1981–1989) in the Chippewa National Forest (CNF) and adjoining George Washington State Forest (47°30'N, 93°30'W) in Itasca County, north-central Minnesota. Additional data (1991–1993) were collected at the Camp Ripley National Guard Training Camp, Morrison County, approximately 170 km southwest of the CNF study area.

The CNF study area was >95% forested, with forest types typical of the northern hardwood / boreal transition. Aspen woods (*Populus tremuloides*) mixed with paper birch (*Betula papyrifera*) and balsam fir (*Abies balsamea*) predominated on the uplands, with lesser amounts of conifer (*Pinus resinosa, P. strobus, Picea glauca*) and northern hardwoods (*Acer saccharum, Tilia americana, Quercus rubra*). Lowland forests of black spruce (*Picea mariana*), tamarack (*Larix laricina*), northern white cedar (*Thuja occidentalis*), and black ash (*Fraxinus nigra*) composed approximately 33% of the forest cover. Upland soils ranged from sandy to silty loams formed on glacial till plains, moraines, and outwash plains (Nyberg 1987). Lowland soils were formed on glacial lake bed sediments and included silts, clays, and deep peat.

Camp Ripley encompassed approximately 215 km² of mixed terrain, including glacial moraine, till plain, and outwash, as well as recent riverine flood plains of the Crow Wing and Mississippi rivers. Vegetation was transitional between the northern mixed forests of the CNF and the central hardwoods. Oak forests (*Q. rubra, Q. macrocarpa, Q. alba, Q. ellipsoidalis*) covered approximately a quarter of the camp. Other common types included aspen–birch, pine (*P. banksiana, P. resinosa, P. strobus*), and maple–birch–oak associations and lowland hardwoods (*Fraxinus* spp., *Ulmus americana, Acer rubrum*). Many hectares were burned annually to maintain open target areas for military training, resulting in interspersed native and non-native grasslands (21% of the camp) and patches of burr oak savanna (4% of the camp). Mean annual rainfall (67 cm) was the same as in the CNF but mean July and January

temperatures were 1–2°C higher and the frost-free period about 17 days longer (National Oceanic and Atmospheric Administration 1993).

Methods

Scat analysis

We collected bear scats from bait sites, trap sites, and garbage dumps and made incidental observations during April–September 1981–1989 in the CNF study area and during April–October 1991–1992 at Camp Ripley. Bait and traps were spread systematically across the study areas, either along linear trap lines that followed roads and trails (about 1 bait or trap per kilometre) or across a trapping grid of about sixty 5.2-km² grid cells (CNF: 1 or 2 trap or bait sites per grid cell). Two garbage dumps were operated in the CNF study area during 1981–1986 and in most years were used by ≥20 radio-collared bears plus an unknown number of unmarked bears. We were not interested, for this analysis, in assessing the contribution of human garbage to the diet of bears, but wished only to determine the relative frequencies and volumes of wild foods in the diet; thus, inclusion of scats from dump sites should not have biased the sample. We collected all scats that appeared to contain at least 50% wild food by volume. Bait and trap sites were checked daily and dumps at least weekly, so scats were ≤1 week old. At Camp Ripley, we also collected fresh scats during observations of human-habituated bears (1 scat per family group observed per day).

Scats were stored frozen prior to analysis. After thawing it, we rinsed each scat through stacked sieves (3.7- and 0.4-mm mesh) to loosen and clean the contents, then determined frequency of occurrence and visually estimated percent volume of ants as 0 or trace or in 5% increments to 100%. For scats containing garbage, we normalized the relative proportions of all non-garbage items to total 100%. We described seasonal changes in the prevalence of ants in scats by grouping half-month periods from late May to early August.

We identified ants in 4 of the 9 years of scat collection from the CNF (1986–1989) and in both years at Camp Ripley. We assigned ants to seven recognizable groups: *Acanthomyops* spp., *Camponotus* spp. (carpenter ants), *Formica* spp., *Lasius umbratus*, other *Lasius* spp., *Myrmica* spp., and all other ants. When >1 type occurred in a single scat, we estimated the relative volume of each. We took sample splits from 1986–1988 CNF scats and all Camp Ripley scats for further identification of all species present.

Ant-nest density and characteristics

To obtain an estimate of the availability of ants in the CNF (both ants in general and specific genera/species), we sampled 22 strip transects, 2 m wide × 532–777 m long, between 18 May and 15 August 1989. Each transect started at a randomly chosen Universal Transverse Mercator map coordinate and followed a random compass bearing; if a body of water was encountered, a new bearing was chosen for continuation of the transect. All cover-type changes along transects were noted. We investigated all stumps, rocks, soil mounds >25 cm in diameter, and woody debris >8 cm in diameter and recorded all ant nests found.

Ants were assigned in the field to 9 species groups, based on obvious morphologic differences: brown *Lasius* spp., yellow *Lasius* spp., large black and red *Formica* spp., other *Formica* spp., *Camponotus* spp., *Myrmica* spp., *Tapinoma sessile*, *Stenemma* spp., and *Leptothorax* spp. These groups were somewhat different from those used in scat analysis, because color and behavior made some distinctions clearer in fresh specimens than in samples from scats, whereas other distinctions were easier to make in the laboratory. For more exact identification and to check field classifications, we collected specimens from 52% of all nests. We found some error in field classification, particularly for *Lasius alienus*

(20% of specimens were field-classified as *T. sessile*) and several uncommon genera, so when we subsequently calculated density for each group, we adjusted estimates according to the proportion of samples incorrectly field-classified.

We computed ratio estimates of 4 variables from the strip-transect data: (1) percentage of the study area composed of each of 9 vegetational cover types (R_{va}), (2) the density of ant nests for each of 9 ant species groups (R_{da}), (3) density of nests for all ant species groups and cover types combined (R_{tda}), and (4) ant-nest density for each cover type (R_{dv}):

$$\hat{R}_{va_i} = \frac{\sum\limits_{j=1}^{22} A_{ij}}{\sum\limits_{j=1}^{22} TA_j} \qquad \hat{R}_{da_i} = \frac{\sum\limits_{j=1}^{22} C_{ij}}{\sum\limits_{j=1}^{22} TA_j}$$

$$\hat{R}_{tda_i} = \frac{\sum\limits_{j=1}^{22} C_j}{\sum\limits_{j=1}^{22} TA_j} \qquad \hat{R}_{dv_i} = \frac{\sum\limits_{j=1}^{n_i} CV_{ij}}{\sum\limits_{j=1}^{n_i} TVA_{ij}}$$

where

$\hat{R}_{va_i}$ is the estimate of the proportion of the area composed of the *i*th cover type

A_{ij} is the area of the *i*th cover type in the *j*th strip

TA_j is the total area of the *j*th strip

$\hat{R}_{da_i}$ is the ratio estimate of nest density for the *i*th ant species group

C_{ij} is the total number of nests of the *i*th ant species group in the *j*th strip

$\hat{R}_{tda_i}$ is the ratio estimate of combined ant nest density from 9 species groups

C_j is the total number of nests, summed over the 9 ant species groups, in the *j*th strip

$\hat{R}_{dv_i}$ is the ratio estimate of total ant-nest density in the *i*th cover type

n_i is the number of strips in which the *i*th cover type occurred

CV_{ij} is the total number of all ant nests found in the *i*th cover type in the *j*th strip

TVA_{ij} is the total area of the *i*th cover type in the *j*th strip in which it occurred

Although several estimators for the variance of a ratio have been described (Wolter 1985, pp. 153−195; Thompson 1992, pp. 191−192), the jackknife variance estimator has been shown to have the most desirable statistical properties (Wolter 1985, p. 171; Wu and Deng 1983). The estimator is computed after drawing all possible subsamples of $n = (k - 1)$ strips from the original sample of k strips and computing a ratio estimate ($\hat{R}_i$) for each subsample. This subsampling procedure was applied to each of the 4 types of ratio estimates and the corresponding jackknife variance estimators were computed as

$$Var(\hat{R}) = \frac{1}{k(k - 1)} \sum\limits_{i=1}^{k} (\hat{R}_i - \bar{R})^2$$

where

$\hat{R}$ is one of the four ratio estimates

k is the total number of strips in the original sample

$\hat{R}_i$ is the ratio estimate from the *i*th jackknife subsample

$\bar{R} = \frac{1}{k} \sum\limits_{i=1}^{k} \hat{R}_i$ = mean of $\hat{R}_i$ values from the k jackknife subsamples

Ninety-five percent confidence intervals on the ratio estimates were computed as

$$\hat{R} \pm 1.96 \times \sqrt{Var(\hat{R})}$$

All computations were accomplished with a SAS macro-program, which is available from M. Riggs upon request.

Density estimates for each field-classified ant group were obtained by means of the above calculations. For individual species within a group, we calculated the density on the basis of that species' frequency in samples relative to frequencies of other species in the group. For example, *C. herculeanus* and *C. novaboracensis* comprised 33 and 67%, respectively, of the *Camponotus* specimens collected. Our estimate of the density of the *Camponotus* group was 18 nests/ha; accordingly, we assigned densities of 6 and 12 nests/ha, respectively, to the two species.

For each ant nest on transects, we recorded the substrate type (soil mound, stump, log, log/soil interface, stump/soil interface) and scored the nest in 5 categories: (1) number of ants visible immediately after the nest was opened (about 1−25, 26−100, or >100); (2) number of eggs, larvae, and (or) pupae visible (about 1−25, 26−100, or >100); (3) predominant size of eggs, larvae, or pupae (0−1, 1−3, >3 mm in length); (4) presence or absence of alates (winged reproductives); and (5) accessibility (easy, moderate, difficult), a subjective assessment of how easily a bear might obtain ants without ingesting large amounts of extra debris. We tested for changes in nest attributes over time and among species by fitting an ANOVA-type mean score model to ordered categorical responses (SAS PROC. CATMOD; SAS Institute Inc., Cary, N.C.). Significant main effects tests were followed by pairwise contrasts among times and (or) species groups. All transects were run between 07:00 and 15:00 on dry days, with diurnal maxima of 16−30°C (National Oceanic and Atmospheric Administration 1989).

Dietary selection

We used three approaches to assess the selectivity of bears feeding on ants. First, we considered that bears' use of different ant species (i.e., frequency of occurrence and percent volume in scats during 1986−1989 in the CNF and 1991−1992 at Camp Ripley) might directly reflect preference if desirable species were common enough that bears' ability to obtain them was not limited by availability (McLellan 1985). Second, using 1989 CNF data, we compared use and availability (density estimates from 1989 strip transects) by testing for concordance between paired use and availability rank scores with Kendall's τ_b coefficient. Values approaching 1 indicate that use varied with availability, implying nonselective, opportunistic feeding, whereas values near zero indicate a lack of concordance between use and availability, implying selective feeding. Finally, using the same data, we calculated Chesson's (1978) index, α, as a measure of bears' preference for different types of ants. Like other use−availability methods, this index assumes that prey-consumption rates are a function of both prey availability and predator preference. From measured use values, it calculates the proportion of the diet that would consist of each prey item if all items were equally available and assumes this new value to represent relative preference. It is more robust to arbitrary inclusion or exclusion of "available" resources than contingency tables or other selectivity indices (Chesson 1978).

At Camp Ripley, we had no measure of campwide ant availability, but on eight occasions during June 1992 and May−July 1993, while observing bears habituated to our presence, we were able to determine the type of ants being consumed. At 3 of those feeding sites, we subsequently sampled 2 m wide strip transects following the approximate foraging path of the bear, allowing us to compare species eaten with species present at those sites.

Nutritional analyses

We determined nitrogen (N) content in worker ants (three species), alates (one species) and pupae (one species), using the micro-Kjeldahl procedure (Association of Official Analytical Chemists 1970). For workers and alates, we subtracted 0.88 from N% before

Table 1. Frequency (%) of occurrence of ants in black bear scats collected from the Chippewa National Forest in north-central Minnesota, 1981–1989.

Year	May 1–15	May 16–31	June 1–15	June 16–30	July 1–15	July 16–31	August 1–15	August 16–31	Sept. 1–30
1981	—	46	67	100	98	100	89	54	46
1982	0	33[a]	38	82	100	70	79	49	26
1983	—	—	17	88	100	83	71	7	12
1984	0[a]	—	60	96	100	89	53	48	0[a]
1985	—	31	73	77	89	64	48	—	33[a]
1986	—	40	73	100[a]	100	92	—	42	67[a]
1987	—	69	73	69	—	—	—	—	0[a]
1988	38[a]	18	67	91	86	—	—	—	—
1989	—	31	57	93	95	—	—	—	—
$\bar{x}$	13	38	58	88	96	83	68	40	26

Note: Sample sizes for the periods reported ranged from 5 to 66. Of 59 periods reported, 52 (88%) had sample sizes ≥10; 33 (58%) had sample sizes ≥20.

[a]Sample sizes ranged from 5 to 9.

calculating crude protein (CP) content, to account for N bound in chitin rather than in digestible proteins (Wigglesworth 1972). We assumed the chitin content of pupae to be negligible. Fat content was determined by ether extraction (Association of Official Analytical Chemists 1980).

We measured total dietary fiber (TDF) (Prosky et al. 1984; Sigma Chemical Co. 1989) and total protein (Henry et al. 1957) in the leaves of 7 common plant foods eaten by black bears during the 4- to 5-week period when bears increased their consumption of ants. Unlike other measures of fiber content, TDF includes soluble, but indigestible, fibers (e.g., gums and pectins), which can represent a substantial portion of omnivore diets (Asp et al. 1983; Halvarson and Alstin 1984), and is a good predictor of digestible energy in diets of non-ruminants (Pritchard and Robbins 1990). Plant material was collected on 22 May, 1 June, 12 June, and 22 June 1989, at 1–5 sites on each date. We gathered foliage from at least 10 plants of each species collected at each site; thus, each specimen analyzed represented a composite sample of a species at a site. Samples were oven-dried at 100°C and ground to a powder for analysis. We tested for changes through time in species-specific CP content and TDF using one-way ANOVA and for changes between consecutive sampling dates at individual sites using Wilcoxon's signed rank tests. To reduce the chance of Type II errors due to small sample sizes, we used $\alpha = 0.1$ for this analysis.

Results

Ant use and availability

Ants were a major seasonal food for bears, both in the CNF and at Camp Ripley. In the CNF, over a 9-year period they occurred in 65% of all scats ($n = 1334$). Mean frequency of occurrence varied from 13% in early May to 96% in early July; in some years ants were present in nearly 100% of the scats collected between mid-June and late July (Table 1). Percent volume of ants in scats was also high; in some years ant remains comprised up to 70 and 82% of scat volume in late June and early July, respectively, and never <33% (9-year mean for early July was 58%; Fig. 1). Ant remains included exoskeletons, pupal cases, and a fine, dark, organic material that occurred most often in conjunction with the yellow ants *L. umbratus, Acanthomyops claviger*, and *A. interjectus* (present in 45% of scats containing only these species versus 13% of scats containing only other ant species).

We suspect that the material originated from ingested nest material; nests of yellow ants often contained chamber walls apparently constructed by the ants of a dark, fine-grained organic material.

The late June – early July peak in ant consumption (Fig. 1) was consistent across years, though the onset of intensive feeding, peak level of consumption, and seasonal duration varied (Table 1). Consumption was tied to spring temperature: in 5 years when the April + May deviation from normal mean temperature was >2.5°C (1981, 1985–1988), early June scats contained 13–43% ants ($\bar{x} = 26\%$), in contrast to 3–11% ($\bar{x} = 6\%$) in years with average or below average temperatures (t test, $P = 0.013$). At Camp Ripley, bears began feeding heavily on ants 4–6 weeks earlier and decreased their feeding 2 weeks earlier than in the CNF (Fig. 1).

In the CNF, one species of small yellow ant, *L. umbratus*, consistently occurred more frequently and in larger volumes in bear scats than did other species (Table 2), accounting for 94, 84, 90, and 89% of ants in scats (by volume) in 1986–1989, respectively. *Camponotus* (mostly *C. noveboracensis*) and *Formica* (mostly *F. subnuda*) species were also fairly common in scats, but in much smaller volumes. We could detect no differences among years (1986–1989) in bears' relative use (frequency of occurrence) of these 3 ant groups ($\chi^2 = 6.1$, df $= 6$, $P = 0.41$). At Camp Ripley, three species of ants, *L. umbratus, A. interjectus*, and *A. claviger*, were prevalent in scats, whereas *F. obscuripes, F. subnuda*, and *C. noveboracensis* occurred at lower frequency and in much smaller volumes (Table 2). In May, most ants eaten by Camp Ripley bears were *A. interjectus* with some *F. obscuripes*, whereas other species were consumed mostly in June and July.

Total density of ant nests in the CNF was estimated at 417 ± 81 (95% CI)/ha and ranged from 32 to 693/ha in individual transects. Variation was often as high within as between cover types, and some types occurred only rarely in transects, so confidence intervals were large and few cover-type differences were apparent (Table 3). The array of ant species was similar across many cover types. We identified 20 species of ants in transects, representing 8 genera, and

Fig. 1. Seasonal changes, by half-month period, in the frequency of occurrence and percent volume of ants and associated material in black bear scats in the Chippewa National Forest, north-central Minnesota, 1981−1989, and Camp Ripley National Guard Training Camp, central Minnesota, 1991−1992.
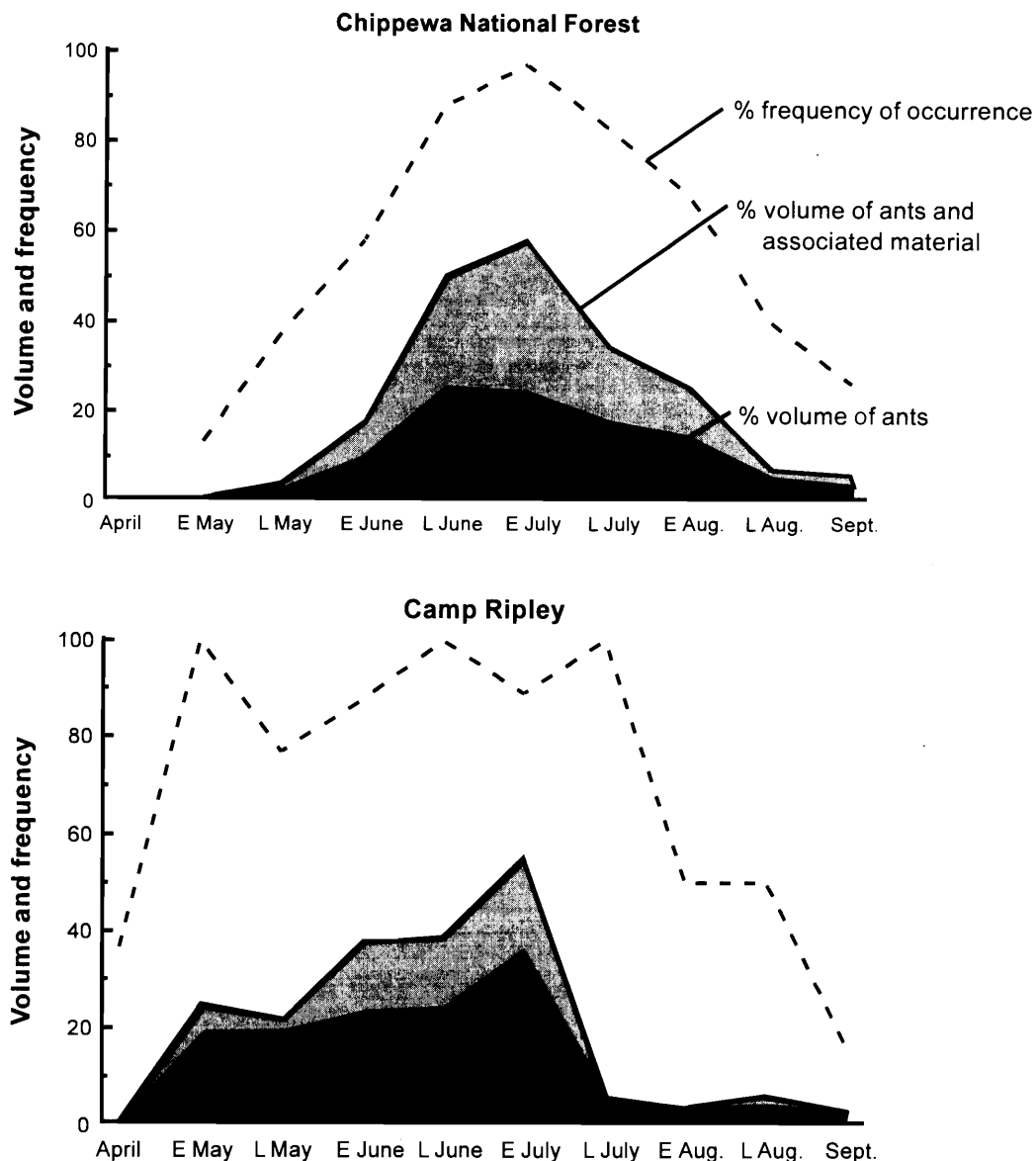
estimated their densities (Table 4). *Lasius* and *Formica* species accounted for 75% of all nests detected, and *L. alienus*, a small brown ant, occupied 33% of all nests. One species, *F. ulkei*, was not identified in transects, but its large, clustered mounds were conspicuous in a few localities in open habitats with high water tables.

The predominance of *L. umbratus* and *Acanthomyops* spp. in bear scats suggested strong selection of these species, and the near absence of *L. alienus*, *F. fusca*, and *Myrmica* spp. suggested avoidance, particularly considering their widespread availability. By collapsing the 20 ant species in transects into the 6 ant groups identified in scats, we were able to compare use and availability in the CNF in 1989. Kendall's rank correlations showed no correspondence between relative density and bears' use of different ant species, measured as either frequency of occurrence ($\tau_b = -0.33$, $P = 0.35$) or relative volume in scats ($\tau_b = -0.15$, $P = 0.69$). This also

suggested that bears were being selective, i.e., not using different ant species in proportion to their abundance. Chesson's preference index was highest for *L. umbratus*, much lower for *Camponotus* and *Formica* species, and 0.0 for other species (Table 5).

Nest characteristics and phenology

Most ant nests in the CNF were found inside the wood or under the bark of partially decayed downed logs (Table 6). *Lasius umbratus*, *L. pallitarsis*, *C. noveboracensis*, and *Myrmica* (*emeryana* complex) sp. tended to colonize stumps and the soil/wood interface more often than did other species ($P < 0.0001$). Nests of *F. subnuda* were more populous than those of other species except *F. neorufibarbis* ($P \le 0.0001$ for all pairwise contrasts); 70% of *F. subnuda* nests were categorized as "large" versus <40% for other ants (Fig. 2). *Camponotus* spp. nests were typically smaller than those of

Table 2. Relative frequency of occurrence of different ant species in black bear scats from the Chippewa National Forest (CNF), 1986–1988, and Camp Ripley, 1991–1992, in north-central Minnesota.

	CNF		Camp Ripley	
	No. of occurrences[a]	Relative frequency (%)	No. of occurrences[a]	Relative frequency (%)
Lasius umbratus	138	70.1	24	26.6
Lasius alienus	1	0.5	—	—
Acanthomyops interjectus	—	—	22	24.4
Acanthomyops claviger	—	—	14	15.6
Camponotus noveboracensis	17	8.6	4	4.4
Camponotus herculeanus	2	1.0	—	—
Formica subnuda	26	13.2	6	6.7
Formica obscuripes	—	—	10	11.1
Formica glacialis	8	4.1	—	—
Formica obscuriventris	—	—	2	2.2
Formica subsericea	—	—	1	1.1
Formica fusca	—	—	1	1.1
Formica fossaceps	1	0.5	—	—
Formica ulkei	1	0.5	—	—
Unidentified *Formica* spp.	—	—	3	3.3
Myrmica lobifrons	1	0.5	—	—
Myrmica detritinodis	—	—	1	1.1
Tapinoma sessile	1	0.5	1	1.1
Leptothorax ambiguus	1	0.5	—	—
Crematogaster cerasi	—	—	1	1.1

[a]Number of scats containing each ant species, out of a total of 165 CNF and 49 Camp Ripley scats that contained ants.

Table 3. Density of ant nests and species distribution in 9 vegetational cover types common to the Chippewa National Forest, north-central Minnesota, 1989.

Cover type	Total. no. of ant nests/ha		No. of transects including cover type	Estimated percentage of land area ($\bar{x} \pm$ 95% CI)	Relative frequency of ant species (percentage of nests in each species group)[a]							Estimated density (nests/ha) of *L. umbratus*[b]
	$\bar{x} \pm$ 95% CI	Range			La	Other L.	Fs	Other F.	Camp	Myr	Other spp.	
Aspen/birch/fir	593±79	90–1080	19	38±15	35	14	4	29	3	13	2	42
Aspen regeneration	474±92	315–645	8	12±10	42	10	3	21	7	16	2	24
Mixed pine	224±110	75–1000	8	9±7	39	17	3	19	5	14	2	19
Upland semi-open	222±500	205–295	2	4±6	16	12	23	15	12	15	7	14
Upland hardwood	476±124	75–650	11	6±3	45	14	3	24	1	14	1	33
Lowland conifer	339±203	35–695	14	10±6	16	12	1	28	7	32	5	21
Lowland hardwood	279±191	15–385	4	8±8	28	9	0	14	7	38	5	13
Open bog	0	—	3	4±5	—	—	—	—	—	—	—	0
Grass/sedge	90±588	0–785	12	8±9	41	15	10	10	10	12	3	7

[a]*La*, *Lasius alienus*; Other *L.*, other *Lasius* spp.; *Fs*, *Formica subnuda*; Other *F.*, other *Formica* spp.; *Camp*, *Camponotus* spp.; *Myr*, *Myrmica* spp.

[b]*Lasius umbratus* represents 51% of samples classified as "other *Lasius*," therefore the estimated density of *L. umbratus* in each cover type is (0.51) × (% of nests in that cover type classified as "other *Lasius*") × (ant-nest density in that cover type); for the aspen/birch/fir cover type, for example, the estimated density of *L. umbratus* is 0.51 × 0.14 × 593 = 42 nests/ha.

Formica spp. or *Lasius* spp. ($P \le 0.006$ for all pairwise contrasts). Nests of *F. subnuda*, *L. pallitarsis*, and *L. alienus* generally had the most pupae visible (Fig. 2) and *Camponotus* spp. and *L. umbratus* nests the fewest ($P < 0.0001$). The largest ants (*Camponotus* and *Formica* species) tended to produce the largest pupae ($P < 0.0001$ for the species main effect).

From May through June, there was a steady increase in both the percentage of ant nests with eggs, larvae, and (or) pupae present and the abundance of these in nests (Fig. 3; $P < 0.0001$ for the season main effect; $P \le 0.005$ for all pairwise contrasts among consecutive periods). Larvae and pupae were most numerous in early July, decreasing somewhat by early August. Small sample sizes made it more

Table 4. Estimates of nest densities for 9 ant species groups in the Chippewa National Forest, based on counts from strip transects made during 18 May − 15 August 1989.

Species group[a]	No. of ant nests/ha ($\bar{x} \pm 95\%$ CI) ($n = 22$)[b]	Identification bias[c]	Species in group[d]	Species composition of group[d] (percentage of nests)	Adjusted density estimate[e] (nests/ha)
Brown *Lasius* spp.	126±37	0.90	*L. alienus*	100	140
Yellow *Lasius* spp.	55±23	0.98	*L. umbratus*	51	29
			L. pallitarsis	44	25
			L. nearcticus	5	3
Large black and red *Formica* spp.	16±11	1.00	*F. subnuda*	84	13
			F. fossaceps	3	<0.5
			F. exsectoides	3	<0.5
			F. whymperi adamsi	3	<0.5
			Formica sp.	6	1
Other *Formica* spp.	106±35	1.01	*F. fusca*	86	90
			F. neorufibarbis	10	11
			F. subsericea	3	3
			Formica sp.	1	1
			Polyergus breviceps[f]	1	1
Camponotus spp.	18±9	1.02	*C. noveboracensis*	67	12
			C. herculeanus	33	6
Myrmica spp.	69±22	1.02	*M. emeryana* complex	60	41
			M. incompleta	36	24
			M. lobifrons	4	3
Tapinoma sp.	24±8	2.24	*T. sessile*	100	11
Stenamma spp.	2±3	1.50	*S. diecki*	100	2
Leptothorax spp.	2±2	0.71	*L. muscorum*	100	3

[a]Where available, laboratory identification was used to assign ant nests to groups for density estimates; where no sample was taken, group assignment was based on field classification.

[b]Twenty-two strip transects were sampled, each 2 m wide and 532−777 m long; total area sampled was about 27 000 m^2.

[c]Identification bias is calculated as (total number of nests identified in field or laboratory in each species group / total expected after adjusting for misclassification), e.g., for *L. alienus*, an identification bias of 0.90 means that the number of ant nests identified as *L. alienus* represents an estimated 90% of the true number in the sample, owing to misidentifications.

[d]Determined from a subset (52%) of nests, sampled for identification to species and verification of field classification.

[e]Estimated nest density for each species, calculated as [(no. of ant nests/ha for the species group) / (identification bias)] (percentage of nests in the group inhabited by that species).

[f]A single specimen was collected and misidentified in the field as *Formica* sp.

Table 5. Calculation of the selectivity index α (Chesson 1978) to determine feeding preferences of bears eating ants, based on measures of ant use (relative percent frequency and relative percent volume in scats) and availability (relative density of ant nests) in north-central Minnesota, 1989.

Ant species	Relative density[a] (%)	Relative frequency in scats[b] (%)	Selectivity index (α_1)[c]	Relative vol. in scats[d] (%)	Selectivity index (α_2)[e]
Lasius umbratus	6.9	63.1	0.62	88.7	0.87
Other *Lasius* spp.	40.0	0.0	0.00	0.0	0.00
Formica spp.	28.4	14.4	0.03	3.9	0.01
Camponotus spp.	4.3	17.1	0.27	7.4	0.12
Myrmica spp.	16.2	1.0	0.00	0.0	0.00
Other	4.1	4.5	0.07	0.0	0.00

[a]Relative density of each ant group (percentage of total nest density).

[b]Relative frequency of occurrence of each ant group in scats (percentage of total occurrences).

[c]Selectivity index calculated as in Chesson (1978); α_1 was calculated using frequency of occurrence as the measure of "use."

[d]Relative volume of each species in scats (percentage of total ant volume).

[e]α_2 was calculated using percent volume as the measure of "use."

Fig. 2. Abundance and accessibility of adult and immature stages in nests of 10 ant species commonly found in the Chippewa National Forest, north-central Minnesota, 1989.
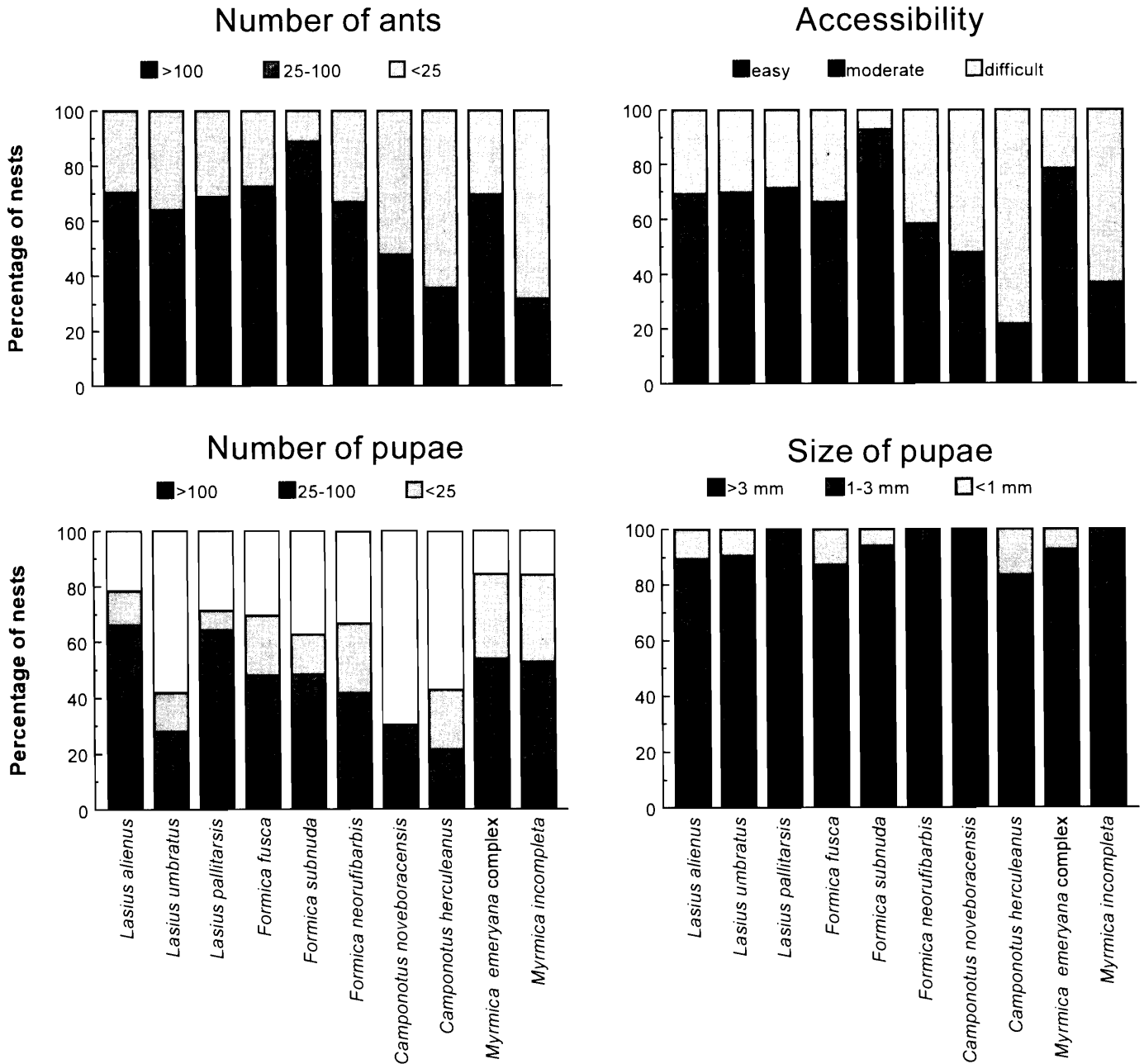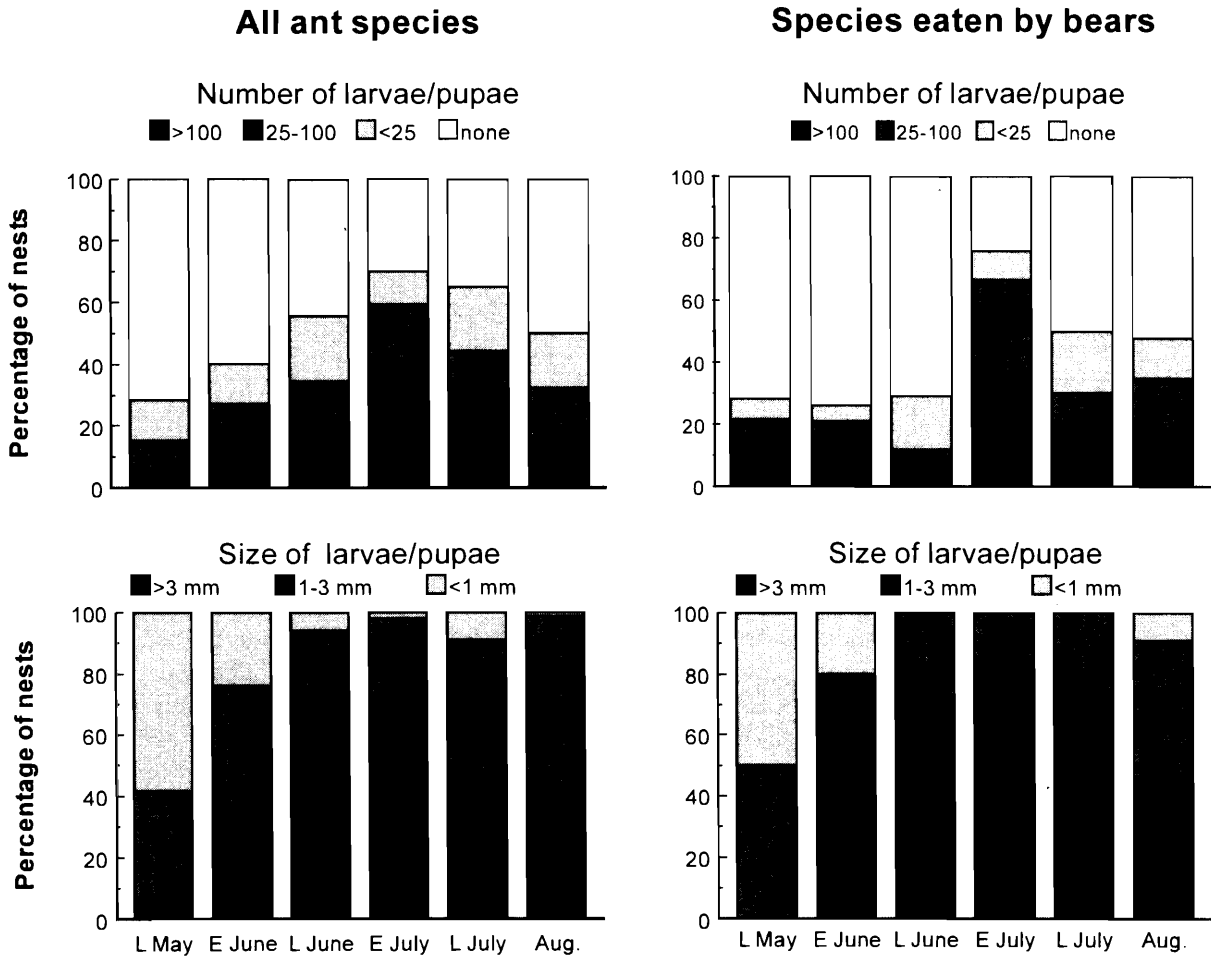

Table 6. Percentages of nests in different substrates for 10 ant species commonly found in the Chippewa National Forest, north-central Minnesota.

Ant species	n	Log	Log/soil	Moss	Stump	Mound
Lasius alienus	157	68	8	3	22	1
Lasius umbratus	50	28	22	8	42	0
Lasius pallitarsis	42	38	31	5	26	0
Formica fusca group	105	60	7	1	29	1
Formica subnuda	27	56	7	0	33	4
Formica neorufibarbis	12	50	0	8	25	17
Camponotus noveboracensis	23	48	17	0	35	0
Camponotus herculeanus	14	57	7	7	29	0
Myrmica emeryana complex	65	62	17	8	12	2
Myrmica incompleta	38	53	5	5	37	0

Fig. 3. Seasonal changes in the size and abundance of available brood in ant nests in the Chippewa National Forest, north-central Minnesota, 1989.

All ant species

Number of larvae/pupae
■>100 ■25-100 ☐<25 ☐none

Size of larvae/pupae
■>3 mm ■1-3 mm ☐<1 mm

Species eaten by bears

Number of larvae/pupae
■>100 ■25-100 ☐<25 ☐none

Size of larvae/pupae
■>3 mm ■1-3 mm ☐<1 mm

difficult to discern patterns for individual species, but for the combined group of species eaten by bears, the seasonal trend was similar (Fig. 3), with significant change occurring between late May and early June ($P = 0.01$). In nests of *L. umbratus* and *L. pallitarsis*, large numbers of pupae persisted through late July, and in *L. alienus* nests, through early August. Size of pupae increased significantly from late May to early June ($P < 0.0001$) and again to late June ($P = 0.0001$), peaking in late June and early July, with 55–65% of nests containing large pupae. Before mid-June and after mid-July, smaller to medium-sized eggs, larvae, and pupae predominated (Fig. 3). Alates were first detected in nests of *Myrmica* spp. and *L. alienus* in late July (7 and 13% of nests, respectively) and appeared in nests of *Formica* spp. (21%) and *Camponotus* spp. (9%) by early August. No alates of other species were detected prior to the end of the sampling period in mid-August.

Formica subnuda appeared to be more accessible and Camponotus spp. less accessible than other species ($P < 0.0001$ for the species main effect; $P \leq 0.02$ for all pairwise contrasts; Fig. 2). Accessibility ratings were influenced by the size and density of workers and pupae, nest structure (ants dispersed or concentrated, firm superstructure or loose soil), and ant behavior. Some species fled and carried off pupae quickly when nests were disturbed (*F. fusca, F. neorufibarbis, L. alienus, Camponotus* spp., *T. sessile*) and

some recruited to the site of disturbance in defense (*F. subnuda, F. ulkei*), whereas some neither fled nor attacked (*L. umbratus, L. pallitarsis, Acanthomyops* spp.) or were slow to evacuate (*Myrmica* spp.).

Though transect data suggested that, on average, *L. umbratus* nests were intermediate in size, pupal population, and accessibility relative to other species, some of the *L. umbratus* nests unearthed by foraging bears contained hundreds of ants concentrated in dense, nearly continuous layers on exposed nest surfaces. Similarly, at Camp Ripley, habituated bears led us to the most densely populated mounds of *Acanthomyops* spp. *Formica ulkei* and *F. obscuripes* were relatively uncommon, but where they were present, occupied prominent, sometimes densely populated, soil mounds.

Observations of ant-feeding behavior by bears
On eight occasions at Camp Ripley, we observed habituated black bears feeding on 38 ant nests; 20 contained *L. umbratus* or *Acanthomyops* spp., 5 contained *F. subnuda*, 8 contained *Myrmica* spp., and 5 contained other species. At 3 of the sites, we knew that the bear fed exclusively on *L. umbratus* or *Acanthomyops* spp., yet when we examined transects (30, 100, and 200 × 2 m) along the bear's travel path, we found that nests of these species constituted only 20% (2 of 10), 40% (4 of 10), and 23% (17 of 75), respectively, of the nests we could find. Most other nests belonged to

Table 7. Nutrient composition (percent dry mass) of ants collected in north-central Minnesota.

		Nitrogen (N)	Crude protein (CP)[a]	CP adjusted for chitin[b]	Ether extract	Ash	Carbohydrate[c]	Cal/g[d]
Acanthomyops spp.								
Workers								
Nest 1	May	6.9	43.0	37.6	33.9	3.8	11.9	5.5
Nest 2	May	6.0	37.4	32.0	28.2	6.6	20.4	5.1
Nest 3	April	4.6	29.0	23.3	—	—	—	—
Pupae								
Nest 1	May	7.0	43.9	43.9[e]	35.7	4.8	15.6	6.1
Nest 2	May	5.8	36.3	36.3[e]	33.5	7.8	22.4	5.8
Camponotus spp.								
Workers	Dec.	6.4	40.1	34.5	19.5	2.0	31.2	4.8
Alates	Dec.	5.1	31.7	26.4	52.7	1.6	6.5	6.5
Formica spp.								
Workers	Dec.	5.2	33.1	27.0	24.0	15.9	20.3	4.4

[a]N × 6.26.
[b](N − 0.88) 6.25, as per Wigglesworth (1972), 12.8% chitin assumed for dry-mass composition.
[c]100 − (% CP + % chitin + % ether extract + % ash).
[d]4.8 (% CP) + 9.5(% ether extract) + 4.2(% carbohydrate).
[e]Chitin content in pupae assumed to be negligible.

L. alienus, with a few occurrences each of *F. subnuda*, other *Formica* spp., and *Camponotus* spp. At 1 site, a bear fed on 4 *Acanthomyops* spp. nests, all containing unusually dense concentrations of ants and pupae. In that transect, only 1 other *Acanthomyops* and 1 *F. subnuda* nest out of 71 nests held such dense concentrations of ants and pupae.

Habituated bears seemed to locate ant nests first by visual cues (e.g., downed logs or stumps), but on approaching, to use smell in determining where to break into nests. At most sites they spent < 1 min feeding, but at very large nests, like the 4 *Acanthomyops* spp. nests mentioned above, feeding time sometimes exceeded several minutes. Nevertheless, the bear feeding at those nests ceased feeding, as was common, long before exhausting the supply of ants and pupae; hundreds were still exposed when she left, and hundreds more were accessible in adjacent parts of the nests. A sample of this bear's stomach contents (regurgitated during anesthesia 2 h after the observed foraging) contained, by volume, 70% worker ants, 15% pupae, and 15% debris (sand and associated fine organic material). Grab samples taken from 2 of the nests contained, by volume, only 30 and 26% worker ants, 5 and 16% pupae, and 65 and 58% debris, suggesting that the bear was able to partially extract ants from surrounding loose material while feeding. Dry mass composition of stomach contents was 48% workers, 19% pupae, and 33% debris, in contrast to 6 and 14% workers, 6 and 10% pupae, and 88 and 76% debris in the nest samples. Eight of 9 nests checked several days after disturbance by bears were still active. Only the nest with the longest observed feeding time (15 min) was subsequently abandoned by the surviving ants.

Nutrient composition of bear foods in spring

N content in ant samples ranged from 4.6 to 7.0% dry mass (Table 7), or 23−38% adjusted CP content in worker ants and 36−49% CP content in pupae. Lipid content was 20−36% in the worker and pupa samples, whereas it was 53% in the alate sample. Results suggested that there may be sig-

nificant differences between nests: mean N content (based on 4 subsamples each) in both workers and pupae differed between 2 *Acanthomyops* spp. nests sampled on the same day ($P = 0.0001$ for workers, $P = 0.01$ for pupae; Table 7); there appeared to be similar differences in lipid content.

All samples of herbaceous foods collected in late May (one composite sample for each of six species) had CP levels >18% and TDF <50% (Table 8). In the June 1 collection, all samples still contained >17% CP (17.3−38.9%), except those of *Maianthemum canadensis*, which contained only 10.1−14.1% CP. However, after June 1, *Aster macrocarpa*, *Populus tremuloides*, *M. canadensis*, and *Trifolium* spp. all showed significant losses in CP sometime before 22 June ($P \le 0.1$), and the data for *Calla palustris* suggested likewise, though only 1 site was sampled.

TDF was higher in all samples of *A. macrocarpa*, *P. tremuloides*, *Calamagrostis* spp., and *Trifolium* spp. collected on June 1 than in the May samples. TDF in *A. macrocarpa* and *Trifolium* spp. increased significantly between early and late June ($P \le 0.1$; Table 8), whereas no such trend was evident for *M. canadensis*, *P. tremuloides*, *Impatiens* spp., or *C. palustris*. By late June, only *Trifolium* spp., *C. palustris*, and *Impatiens* spp. maintained CP content ≥17% and TDF ≤50%.

Discussion

Dietary selection and characteristics of preferred ant prey

Ants, particularly yellow ants, were an important seasonal food for bears in both central and north-central Minnesota, occurring in scats in high volume and frequency for 4−8 weeks annually. Even after ripe berries became abundant in mid-July (Noyce and Coy 1990), ants continued to occur frequently, though in reduced volumes. Observations of habituated bears at Camp Ripley indicated that as early as mid-May, 60% of bears' foraging time was spent in pursuit of ants, increasing to 80−100% during June (Ternent 1995).

Table 8. Crude protein content (%) and total dietary fiber (%) in herbaceous spring foods of black bears in north-central Minnesota, 1989.

	22 May			1 June			12 June			22 June			$P \le 0.1^a$	
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	ANOVA	Signed rank
Crude protein content														
Populus tremuloides														
Early	26.9	—	1	25.0	1.4	5	17.1	0.9	5	14.4	1.3	5	*ac*	*abc*
Late	—	—	—	38.9	—	1	—	—	—	25.3	2.2	4		
Aster macrocarpa	30.1	—	1	30.4	1.8	3	20.2	2.5	5	15.6	1.9	5	*ac*	*b*
Trifolium spp.	25.4	—	1	25.8	0.6	5	25.7	0.8	5	21.4	0.3	5	*bc*	*bc*
Maianthemum canadensis	21.8	—	1	11.9	0.7	5	11.1	0.3	5	9.5	0.4	5	*bc*	*bc*
Calla palustris	—	—	—	26.0	—	1	20.1	—	1	16.9	—	1		
Impatiens spp.	18.4	—	1	23.9	—	1	19.0	—	2	17.9	—	2		
Calamagrostis spp.	17.7	—	1	17.3	—	1	19.3	—	1	18.1	—	1		
Total dietary fiber														
Populus tremuloides														
Early	41.7	—	1	60.2	0.7	5	64.3	0.7	5	61.4	0.7	5	*ab*	*ab*
Late	—	—	—	49.3	—	1	—	—	—	—	—	—		
Aster macrocarpa	43.7	—	1	51.9	0.6	3	58.4	1.1	5	59.9	0.4	5	*ac*	*b*
Trifolium spp.	38.3	—	1	42.7	0.4	5	45.7	0.6	5	49.8	1.9	5	*bc*	*abc*
Maianthemum canadensis	46.4	—	1	45.8	1.1	5	44.6	1.1	5	44.7	2.2	5		
Calla palustris	—	—	—	41.1	—	1	41.9	—	1	41.7	—	1		
Impatiens spp.	42.2	—	1	36.1	—	1	41.5	—	2	46.5	—	2		
Calamagrostis spp.	49.7	—	1	53.8	—	1	61.1	—	1	60.9	—	1		

Note: On each date, for each species sampled, plant material was gathered from ≥ 10 plants at each collection site and combined to form a composite sample for analysis.

^{a}Letters denote pairs of collection dates that are significantly different: a, 1 June/12 June; b, 12 June/22 June; c, 1 June/22 June.

Our data suggested that cover type may not be a good predictor of locations where bears can find ants. *Lasius umbratus*, the preferred species in the CNF, was available in many cover types. In semi-open uplands, where *L. umbratus* was perhaps less common, *Camponotus* spp. and *F. subnuda* were abundant, and only open areas devoid of woody debris were clearly lacking in nests. Size, abundance, and condition of woody debris may be important determinants of ant density (Johnson 1996) and bears may focus on specific sites, rather than specific cover types, where they can find large nests of desirable species.

The yellow ants *L. umbratus*, *A. interjectus*, and *A. claviger* share several traits that may explain their particular attractiveness to bears. They sometimes form dense concentrations inside nests, workers are slow to evacuate brood when disturbed, and they display a passive defense response, i.e., workers neither flee nor attack. Their citronellal and other alarm/defense pheromones (Blum et al. 1968) appear to have little effect on bears, who may even use the strong, distinctive odor to help locate nests. We have been able to detect freshly disturbed nests up to 10 m away.

The combination of strong odor, populous colonies, and passive behavior is not shared by other ants in north-central Minnesota. Other *Lasius* species do not excrete citronellal, and worker densities are not as high as in some *L. umbratus* nests. *Lasius alienus* is very quick to seek cover when disturbed. *Tapinoma sessile* and *F. fusca* likewise have relatively small nests and flee from disturbance immediately. *Myrmica* spp. are fairly sluggish when disturbed but generally live in nests with small numbers of workers and pupae.

Camponotus spp., *F. subnuda*, and other large *Formica*

spp. may be more attractive to bears than some smaller species because of their large size. However, *Camponotus* spp. nests typically require more work to penetrate than those of *L. umbratus* and likely provide less nutritional return for the effort, as workers move brood to safety very quickly. *Formica subnuda*, *F. ulkei*, and *F. obscuripes* can have dense nest populations, but they too evacuate brood quickly. Those ants that remain at the site mount an aggressive defense (biting, then spraying with formic acid), which may help limit the frequency or duration of predation by bears, as Redford (1987) suggested for other mammalian myrmecophages. Chimpanzees curtail feeding on *Camponotus* spp. nests after the ants attack (Nishida and Hiraiwa 1982), and chemical defenses influence both prey preference and feeding duration in many ant-eaters (Lubin and Montgomery 1981; Redford 1985; Abensperg-Traun 1988). Even taste may influence prey consumption; captive armadillos (*Dasypus novemcinctus*) reduced food intake when formic acid (high levels of which are found in *Formica* and *Camponotus* species) was added to rations (Maller and Kare 1967). Though bears regularly endure stings when feeding on wasp and bee brood, and it seems unlikely that they would be repelled by biting ants, they may opt to avoid discomfort when a choice between aggressive and passive ant prey is available. The longest feeding bouts we observed were at nests of passive species.

Regional differences in ant consumption

Although numerous studies have identified ants as the predominant insect food of black bears, the large volume consumed by bears in north-central Minnesota appears to be a

local phenomenon. Regional differences are likely related to the species being consumed. Our observations suggest that bears feeding on yellow ants can ingest a larger volume per unit time than those feeding on other species.

In five black bear studies performed outside the Great Lakes region, where the ant species in scats were identified, *Camponotus* spp. occurred most commonly and neither *L. umbratus* nor *Acanthomyops* spp. were reported (Graber and White 1983; Grenfell and Brody 1983; Maehr and Brady 1984; Smith 1984; Irwin and Hammond 1985; Schwartz and Franzmann 1991), though Schwartz and Franzmann (1991) noted an unidentified species of *Lasius* in bear scats in Kenai, Alaska. Grizzly bears (*Ursus arctos*) were also reported to eat mostly *Camponotus* spp. (Knapp 1979[1]; Hamer and Herrero 1987; Mattson et al. 1991), but not *L. umbratus*. In these and other studies (Tisch 1961; Landers et al. 1979; MacHutchon 1989; Beeman and Pelton 1980; Clapp 1990; Holcroft and Herrero 1991; Hellgren 1993), ants, though often frequent in scats, never exceeded 26%, and were usually <15%, of scat volume, even during peak periods of use. Only at Banff Park (Raine and Kansas 1990), where ants composed 48% of scat volume during July, did ant abundance in bear scats approach that in this study; however, the species consumed were not specified.

Lasius umbratus and *Acanthomyops* spp. appear to be rare in black bear habitat in western and southeastern North America, where all the above studies were conducted. Wheeler and Wheeler (1980)[2] acknowledged their possible occurrence in Yellowstone National Park, but collected no specimens during a parkwide survey. Knight et al. (1981) found *Acanthomyops* spp. at several grizzly bear feeding sites, but not in scats. *Lasius umbratus* may occur in southern portions of the Canadian Prairie provinces and in some western states, but not in British Columbia or the Pacific Coast states (Wilson 1955). Five species of *Acanthomyops* (not *A. claviger* or *A. interjectus*) have been recorded infrequently from western Canada (Wing 1968), nesting mostly in grasslands or open woods under rocks or boulders.

Conversely, *Camponotus* spp. are among the most common and widely distributed ants in the world, with several species dominant in the coniferous forests of North America (Wilson 1976; Redford 1987). Forest cover is predominantly coniferous in Yellowstone National Park (Mattson et al. 1991), southern Alberta (Hamer and Herrero 1987), and California (Grenfell and Brody 1983), where *Camponotus* spp. were common in bear scats; in Alaska's Kenai Peninsula, forest fires in the mid-1900s left high densities of conifer snags and woody debris ideal for *Camponotus* spp. colonization (Schwartz and Franzmann 1991).

In Minnesota, the south-to-north transition in the species and relative volumes of ants consumed by bears likely illustrates an interaction between prey species abundance and prey preference. At Camp Ripley, *Acanthomyops* spp. and *L. umbratus* all provided efficient foraging and were consumed in large volumes. *Acanthomyops claviger* and *A. inter-*

jectus reach their northern extent in Minnesota between Camp Ripley and the CNF (Wing 1968; Gregg 1946), whereas *L. umbratus* extends into the CNF, where bears ate it almost to the exclusion of other available species, including those of *Camponotus*. Farther north, in the Superior National Forest, all three yellow ant species are likely absent or scarce (Gregg 1946). Conversely, *Camponotus* spp. are likely more abundant, since spruce and fir, the trees they most commonly colonize (Sanders 1964, 1970), increase in abundance to the north. Bears there foraged primarily on *Camponotus* spp., the largest bodied ants available (Rogers et al. 1988; Rogers 1989), which they obtained mostly from balsam fir trees killed by spruce budworms (Rogers et al. 1988); budworms affect hundreds of hectares each year in northern Minnesota, but not as far south as the CNF (J. Albers, Minnesota Department of Natural Resources, personal communication). These bears apparently were not able to obtain as many ants as bears in our study that fed on yellow ants, despite spending up to 75% of their foraging time searching for ants (Rogers 1976). During 1970–1977, in samples from the Superior National Forest, all colonial insects composed 16% of the July–August scat volume (Arimond 1979), and in 1988, ants composed 11% of scat volume in July (Rogers 1989).

Nearby, in Michigan's Upper Peninsula, DeBruyn (1992) reported the occurrence of *L. umbratus* in bear scats, but not the frequency or volume relative to those of *Camponotus* spp. Johnson (1996) reported that two habituated bears in that study selected *L. umbratus* over other species, but one also selected *Camponotus* spp. and *F. subnuda*. *Lasius umbratus* was likely less common there than in north-central Minnesota; while Johnson (1996) found it at bear feeding sites, Wheeler et al. (1994) recorded neither *L. umbratus* nor *Acanthomyops* spp. in the Upper Peninsula. Accordingly, ants composed a July maximum of only 8 and 20% of scat volume for bears in that study during the 2 years reported (DeBruyn 1992). We recognize that high relative volumes of ants in scats could result from low rates of consumption of other foods; however, this cannot explain differences observed across the Great Lakes region, where spring vegetation is not in short supply.

Nutritional ecology of ant-feeding

In north-central Minnesota, spring is a time of growth for young bears (Noyce and Garshelis 1997). Growth requires protein, but also energy to make use of protein. Succulent spring plant foods provide protein, but little fat or carbohydrate to provide the energy. Dietary protein can be metabolized for energy, but only at the expense of amino acids that could otherwise be used for body protein. Bears with body fat remaining after hibernation likely use that fat to support growth (Noyce and Garshelis 1997), but they also seek high-energy foods in spring, if these are available. Ants, even in small amounts, provide protein and perhaps essential amino acids unavailable in other spring foods (Eagle and Pelton 1981; Redford and Dorea 1984). They may, however, be equally important as a source of energy. The stomach contents we sampled from a Camp Ripley bear contained ≥0.5 kg of *Acanthomyops* spp. remains from a single feeding period. Adjusted for water content (65.5%), this represented approximately 38 g protein, 28 g fat, and 18 g

[1] M. Knapp. 1979. Grizzly bear feeding activity on ants. Senior thesis, Colorado State University, Fort Collins.

[2] G.C. Wheeler, and J. Wheeler. 1980. Research report on ant species within Yellowstone Park and adjacent area. Unpublished report, University of Nevada, Reno.

carbohydrate, or 575 calories gross energy, assuming no nutritional content in what we presume to be ingested chamber material. We believe it possible that in north-central Minnesota, the availability of ant species that bears can consume in large quantities could contribute to the higher spring growth rates we see in young bears relative to those reported in other locations (Noyce and Garshelis 1997).

Declines in protein levels and increases in TDF (inversely related to digestible energy (Pritchard and Robbins 1990)) in plant foods likely encouraged the bears to make a dietary shift to ants in late spring. Minnesota bears stopped feeding on aspen leaves and many woodland herbs as they matured (Rogers 1989; this study), but continued feeding on species (e.g., clover, jewelweed, and wild calla) that remained relatively low in fiber (<50%) and high in protein (≥17%).

Plant phenology cannot, however, explain why bears did not start feeding on ants earlier in the spring. Knight et al. (1981), and later Rogers (1989), hypothesized that bears fed most intensively on ants when eggs, larvae, and pupae were abundant in nests, though this was not documented in either study. Other myrmecophages appear to increase predation on termite nests and to be more tolerant of termite attack when alates are present (Lubin and Montgomery 1981; Griffiths and Simpson 1966). Captive echidnas consumed ant workers belonging to the genus *Iridomyrmex* only if eggs were present (Abensperg-Traun et al. 1991).

Consistent with this hypothesis, bears in this study increased their consumption of ants when numbers of pupae in nests began to increase, and peak consumption coincided with the highest abundance and largest size of pupae. The early onset of ant-feeding in the CNF in years with above-normal spring temperatures may reflect earlier availability of brood in those years, as nest phenology and brood development are tied closely to temperature (Brian 1963; Elmes and Wardlaw 1983). Likewise, the seasonal shift in the ant species consumed by Camp Ripley bears may reflect the availability of pupae; *A. interjectus* and *F. obscuripes* produce the large pupae of reproductive castes in early spring, with mating flights usually occurring in June and (or) July, whereas pupae of the reproductive castes of *A. claviger* do not appear until midsummer, with flights usually occurring in August and September (Talbot 1963, 1972).

Data on ants are scarce, but larvae and pupae of other insects tend to have higher fat (up to 90% dry mass) and total N (5–15% dry mass) levels than most adults (Southwood 1973; DeFoliart 1975; Redford and Dorea 1984). In this study, the estimated energy content of pupae from two nests was 11 and 14% higher than that of workers from the same nests.

However, these differences were small relative to between-nest differences in both pupae and workers (Table 7). While differential digestibility may still make pupae significantly more nutritious than workers, the availability of pupae alone seems insufficient to explain the onset of ant-feeding, particularly as the pupae of *L. umbratus* are not abundant in nests until July (Wheeler and Wheeler 1963; this study). In this study, even worker ants contained more gross energy per gram dry mass than fruits, and certainly more than vegetation. The energy content of workers themselves may change during spring as the general nutritional status of colonies improves following the long winter dormancy (Brian 1970).

Sanders (1972) found that in *Camponotus* spp., during the period of maximal growth of larvae in nests (June – early July), workers spent more time foraging than later in July, which suggests that the number of workers engorged with honeydew may shift seasonally for aphid-tending species (e.g., *L. umbratus*, *Formica* spp., and *Camponotus* spp.) and could result in seasonal changes in the caloric content of workers. The considerable variation in nutritional content of our ant samples and those in other studies (Southwood 1973; Griffiths and Simpson 1966) suggests that further study is necessary to determine if there are seasonal changes in ant nutritional content that could influence feeding patterns of mammalian myrmecophages.

The tendency for bears to feed briefly at many nests, often leaving many ants uneaten, may help them maximize the relatively small nutritional returns available at each nest. Bears may be able to ingest more ants per unit time and (or) a higher ratio of brood to adults than by feeding for longer periods at fewer sites. This behavior is equivalent to partial consumption of prey, by which predators maximize energy intake per unit handling time, particularly when feeding on prey (like ants) that require relatively little energy expenditure for search and capture (Sih 1980; Redford 1985). An additional advantage may be that ant nests are thereby incidentally preserved for future use. Arboreal ant-eaters commonly crop only a portion of the ants available in a nest and rarely do significant damage to colonies (Montgomery 1985a, 1985b). Chimpanzees (Nishida and Hiraiwa 1982) and anteaters (*Tamandua* spp.) (Lubin and Montgomery 1981) regularly revisit nests they have fed on. Black bears in this study revisited nests, most of which appeared to recover from bear attacks. Nest structure and ant behavior may help protect ant colonies from annihilation. Honey ant (*Myrmecocystus* spp.) nests extend below a soil hardpan that mammalian predators cannot penetrate (Chew 1979). *Camponotus* spp. build dispersed galleries inside firm wood that is difficult to breach. A single colony of *Lasius minutus*, a mound-forming species of the eastern United States similar in social organization to *L. umbratus*, may include several to many adjacent mounds that are interconnected (Kannowski 1959). The same colony structure has been recorded for *L. umbratus* in eastern North Dakota (P.B. Kannowski, unpublished data). Even if several mounds are attacked, others can supply ants to rebuild the damaged nests and keep the colony viable.

Clearly, in this study, once fruits became widely available to bears in midsummer, they provided a more accessible source of calories than ants, and the diet shifted accordingly, despite the fact that alates, which are typically higher in fat content than workers or pupae (Redford and Dorea 1984; this study), became available. Nevertheless, bears continued to feed on small volumes of ants and other insects, particularly Vespidae, in late summer and fall (Ternent 1995; K.V. Noyce, unpublished data), perhaps to obtain protein, fat, or particular vitamins or minerals lacking in fruits. Nishida and Hiraiwa (1982) suggested this explanation for the persistence with which chimpanzees "fished" for carpenter ants despite ingestion rates too low to provide a significant caloric return.

For most ant-eating mammals, ants occur in the diet <50% of the time and ant-feeding is likely opportunistic and nonselective (Redford 1987). Even obligate myrmecophages

are not always selective (Abensperg-Traun 1988), and it has usually been assumed that black bears behave similarly. In our study, the distinct seasonality of ant-feeding by black bears, the large volumes ingested, and the bears' preference for a few select species revealed a foraging habit that was both directed and highly selective.

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