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SELECTION OF ANTS BY THE AMERICAN BLACK BEAR (*URSUS AMERICANUS*)

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ABSTRACT.—We examined selection of ants as food by black bears (*Ursus americanus*) in Utah by comparing the genera of ants we sampled from study plots in 5 vegetation types with those found in bear scats. In the plots we found 641 ant colonies representing 18 genera. Five genera comprised 85% of all colonies sampled: *Formica, Lasius, Camponotus, Tapinoma,* and *Myrmica.* Thirteen genera were found in scats, but 99% were composed of the same 5 listed above. Limited utilization of some ant genera by black bears may reflect body size, colony size, nest type, and presence or absence of a functional sting. Fifty-three percent of all ant colonies in sample plots were found under rocks. Energy values of ants ranged from 4.9 to 6.2 cal · g^{-1} dry weight. Pupae of *Formica* and *Camponotus* contained slightly more fat than respective workers, but the relationship was reversed for *Lasius.* Pupal cases were found in 33% of the scats, and bears may prefer ant brood because they are more digestible than adults and lack mechanisms of defense. Ants are a predictable and ubiquitous food source for black bears.

Key words: myrmecophagy, ants, black bears, selective foraging, nutrition, ant colonies.

Although ants (Fomicidae) have been recognized as a component of black bear diets throughout North America (Bigelow 1922, Tisch 1961, Hatler 1972, Landers et al. 1979, Beeman and Pelton 1980, Graber and White 1983, Maehr and Brady 1984, Rogers 1987, Raine and Kansas 1990, Johnson 1996, Noyce et al. 1997), few authors have identified ants found in scat below the family level (for exceptions see Johnson 1996, Noyce et al. 1997, Swenson et al. 1999, Mattson 2001). Because black bears expend considerable energy and time foraging for ants, these insects appear to be an important food item (Rogers 1987, Raine and Kansas 1990, Noyce et al. 1997), at least seasonally; yet, little is known about species preferences or habitats associated with ant consumption by bears. In this study we compare the genera of ants eaten by bears with the relative abundance of these genera in various vegetation types in bear habitat. We also report size diversity and distribution of nest types.

STUDY AREA

The study was conducted on the LaSal Mountains of southeastern Utah where the black bear population is managed by the Utah Division of Wildlife Resources (UDWR). This is a hunted population and, as suggested by a sustained harvest, a stable one as well (Bates and Henry 1999). This semi-isolated mountain range lies between latitudes 38°15′ and 38°40′N and between longitudes 109°00′ and 109°30′W. Elevation ranges from 1690 m to 3914 m. Lower canyons and plateaus are rather xeric with mean annual precipitation <250 mm, while higher elevations may receive annual precipitation of >3000 mm per year. Precipitation at 2130 m measured over a 45-year period averaged 322 mm, with maximum moisture in the form of rain occurring from July through October. May and June are the driest months, averaging 20 mm and 17 mm, respectively (Richmond 1962). Richmond (1962) characterized and mapped major vegetation types along the climatic gradient that are easily recognizable and similar to the life zones of Merriam (1898).

METHODS

We sampled in the 5 most common and extensive vegetation zones throughout the mountains, all of which are utilized by black bears as foraging habitat (Richmond 1962, Richardson 1991). These zones include spruce-fir, aspen

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TABLE 1. Major vegetation types sampled, number of plots, total area sampled, and total area in each vegetation type on the LaSal Mountains, UT, above 1829 m and below alpine tundra.

Vegetation types	# of sample plots	Search time (min)	Area sampled (ha)	% total area sampled	Available habitat (ha)	% total available habitat
Aspen	21	368	0.365	14.0	15,750	20.0
Oak–Mountain brush	19	474	0.693	26.5	18,620	23.6
Pinyon-Juniper	23	557	0.536	20.5	24,670	31.3
Ponderosa	16	398	0.492	18.8	10,530	13.3
Spruce-Fir	23	349	0.527	20.2	9,300	11.8
TOTALS	102	2146	2.613	100	78,870	100.0

meadow, oak–mountain brush, ponderosa pine, and pinyon-juniper communities (see Richardson 1991 for a list of common plants in the study area). These 5 vegetation types comprise 81.6% of the area above 1829 m. We did not search for ants in alpine tundra and sagebrush communities, which make up 2.6% and 15.8%, respectively, of the area above 1829 m (Table 1). We searched for ant colonies from May to August 1989 in 102 nonrandomly selected rectangular plots. Plot size averaged 256 m^2 and the total area sampled was 26,136 m^2. The 5 common vegetation types were sampled unevenly for logistical reasons. From a digitized vegetation map (Richmond 1962), we derived total available area for each major habitat type (Table 1). We overturned rocks that were fist-sized or larger and searched the perimeters of rocks too large to move. We searched under litter using a garden rake as necessary, turned cow pies, and opened logs and stumps using a hatchet. Plots were searched until all substrates thought to contain ants were investigated. Colonies were defined as aggregations of adult ants accompanied by brood (eggs, larvae, and pupae); however, we counted as colonies aggregations where, though brood was not found, nest entrances were accompanied by active workers. When nests were present we recorded nest construction type (e.g., under rock, in wood, or in dirt or thatch mounds) and preserved ants from each colony in 70% ethanol. Identification to genus was made using keys of Allred (1982) and Wheeler and Wheeler (1986). For representative samples of each genus, we measured body length in natural posture to the nearest 0.5 mm.

During 1988 and 1989 black bear scats were collected as encountered. Scats were air- or oven-dried. From the scats containing >1% ants by volume, we randomly selected and weighed 100, and most were one-eighth sampled as follows: each scat was fragmented until it would pass through a 1 × 1-cm mesh screen. Fragments were placed on a 46-cm^2 cloth on which lines connecting diagonal corners had been drawn. Two opposite corners were brought together over the center of the cloth. Holding the 2 corners together, we lifted the cloth off the table, gently shook it vertically 5–7 times, and then laid it flat. The other 2 corners were brought together over the center and the cloth was shaken as before. Three or 4 repetitions of this shaking sequence ultimately centered the scat on the cloth in an elliptical pile. We bisected the scat perpendicular to the length of the pile with a ruler, using the diagonal lines as a reference. One half was removed and the remaining half was shaken and bisected as before. We repeated this procedure until a one-eighth sample of the original scat was obtained. Fourteen of the smallest scats were one-fourth sampled. Samples that deviated more than 2 g from their expected mass, calculated from dry mass of the entire scat, were recombined with the rest of the scat and resampled.

Ant head capsules were removed from the samples, identified to genus, and counted with the aid of a dissecting microscope. We assumed that <20 head capsules per genus per scat sample indicated incidental ingestion; thus, we did not include those samples in the analysis. Head counts of each sample were multiplied by the appropriate factor (8 or 4) to estimate total number of ants per scat. Presence or absence of alate head capsules or pupal cases in each scat was recorded. *Acanthomyops* specimens were combined with *Lasius* because these genera were impossible to distinguish when maxillary palps were broken off during digestion or scat preparation. Additionally, we collected vomitus from a snared bear that contained undigested workers, larvae, and pupae. The specimen was preserved in 70% ethyl alcohol and individual ants were identified and counted.

Nutritional composition of the 5 ant genera was assayed according to standard procedures of the Association of Official Analytical Chemists (Williams 1984). Percent water was determined by drying fresh samples to a constant weight at 105°C. Crude fiber content was measured after digestion of a sample with 1.25% H_2SO_4 and 1.25% NaOH solutions. Total nitrogen content was determined using the semi-automated Kjeldahl method. Fat content was measured directly using anhydrous ether extraction. Finally, ash content was measured after incineration at 525°C. Sufficient sample material was not available to determine ash content of *Tapinoma* or *Myrmica.*

Other nutritional parameters were calculated as follows. For pupae, we multiplied total nitrogen by the constant 6.25 to obtain crude protein (CP). For workers, 0.88 was subtracted from %N before calculating CP to adjust for nitrogen bound in the indigestible chitin of the exoskeletons (Wigglesworth 1972, Noyce et al. 1997). We determined percent carbohydrate by difference (100 minus the sum of crude protein adjusted for chitin, fat, and ash). An estimate of energy content was calculated using the following conversion factors: 4.8 cal $\cdot$ g^{-1} crude protein, 9.5 cal $\cdot$ g^{-1} fat, and 4.2 cal $\cdot$ g^{-1} carbohydrate.

RESULTS

Ant Availability

We searched 102 plots, a total of 35.8 ha, and found 641 ant colonies representing 18 genera. Ninety-two percent of our sample plots contained colonies, and 85% of the colonies were *Formica*, *Lasius*, *Tapinoma*, *Myrmica*, or *Camponotus.* Three genera—*Stenamma, Myrmecocystus,* and *Crematogaster*—were found only once. Brood was found in 92.4% of the colonies.

Genus richness was greatest in pinyon-juniper where 15 genera were found and least in aspen where 6 were found (Table 2); however, mean colony density in pinyon-juniper was slightly lower than that in aspen, oak–mountain brush, and ponderosa pine. Six genera were unique to pinyon-juniper habitat. Habitat had a significant effect on colony density (ANOVA, $P = 0.009$, df = 101, $F = 3.569$), with aspen habitats having a significantly greater mean colony density (450 colonies $\cdot$ ha^{-1}) than spruce-fir habitats (170 colonies $\cdot$ ha^{-1}) as indicated by Tukey pairwise comparisons. Six genera were found in all vegetation types ranging from low-elevation pinyon-juniper to high-elevation spruce-fir (Table 2). *Formica* and *Lasius,* the most common genera found, were more evenly distributed between habitats than were *Myrmica, Camponotus, Leptothorax,* and the small *Tapinoma* (Table 2). High-elevation spruce-fir contained only 12.6% of the colonies. Nearly half of all colonies sampled were in either aspen (n = 152) or oak–mounain brush (n = 151).

Colonies under rocks were common in all habitats (Table 3). Colonies under wood (primarily deadfall) and in rotting and live woody tissue were most common in aspen and spruce-fir. Litter (mainly leaves) provided little suitable habitat for colonies and was even less important than cow dung. Mound colonies were distributed throughout all habitats but constituted only 10.3% of colonies found.

Only *Pogonomyrmex* was not found to establish colonies under rocks (Table 4). This genus is characterized by elevated rock/soil mounds that are conspicuous, devoid of vegetation, and important in thermoregulation of the colony and in incubation of brood. Five rare genera in our sample were found only under rocks. *Formica* utilized all nest types as did *Myrmica.*

We found anecdotal evidence of bears searching for ants and other insects in opened logs, stumps, thatched mounds, and turned cow dung and rocks. Of rocks turned by bears, we observed that 1 was estimated to weigh 139 kg, but smaller rocks, some weighing <0.5 kg, were the norm. On 1 trail nearly every rock was turned for about 150 m, but we found that most rocks did not have evidence of ant colonies under them (e.g., no ants, galleries, or chambers).

Ant Utilization

We collected 791 bear scats, 309 of which contained >1% ants by volume. We randomly selected 100 of these for analysis. Although 13 genera were identified in scats, *Formica, Lasius, Tapinoma, Myrmica,* and *Camponotus* comprised 85% of ants utilized by bears. Scats contained a mean of 3.1 ± 1.8 (s) ant genera

TABLE 2. The percent of ant colonies by genus found in 5 habitat types in the LaSal Mountains, UT. Percentages under the habitat heading sum to 100% within rows.

		% of colonies by habitat				
Genus	Colonies	Pinyon-Juniper	Ponderosa	Oak–Mountain brush	Aspen	Spruce-Fir
Acanthomyops	3		33.3	66.7		
Aphaenogaster	4	75.0		25.0		
Camponotus	51	62.8	7.8	5.9	9.8	13.7
Conomyrma	2	100.0				
Crematogaster	1	100.0				
Forelius	11	81.8	18.2			
Formica	178	11.8	17.4	30.9	25.3	14.6
Lasius	155	7.7	26.5	21.9	23.2	20.7
Leptothorax	30	10.0	10.0	6.7	56.7	16.7
Liometopum	4		100.0			
Monomorium	11	100.0				
Myrmecocystus	1	100.0				
Myrmica	84	2.4	28.6	11.9	46.4	10.7
Pheidole	9	100.0				
Pogonomyrmex	4	100.0				
Solenopsis	16	37.5	12.5	50.0		
Stenamma	1					100.0
Tapinoma	76	11.8	26.3	47.4	13.2	1.3
ALL GENERA	641	19.5	20.6	23.6	23.7	12.6

each. The genus *Polygerus,* though found in scats, was not identified in the colony sampling. We identified alate forms from these 5 genera in 34% of the scats. Pupal cases were found in 33% of scats, but they were often empty and fragmented, making detection difficult. Twelve percent of scats had both alate and pupal forms. Counting of ant heads was straightforward; *Formica* yielded the highest median number of individuals per scat as well as the most individuals recorded in a single scat (Table 5).

Nutritional Considerations

Fat content of ants in our sample ranged from 20.3% to 46.0% (Table 6). The value for *Lasius* was the highest and that genus is the most energy rich among those sampled at 6.2 cal · g^{-1}. Energy values for workers of *Formica* and *Camponotus* were both 4.9 cal · g^{-1} and were approximately 20% lower than *Lasius.* Pupae of *Formica* and *Camponotus* contained slightly more fat than respective workers, but workers of *Lasius* contained substantially more fat than their pupae (Table 6).

DISCUSSION

Ant Availability and Utilization

Although 18 ant genera were distributed across a large elevation gradient and within rather distinct habitats, only 5 genera were important as prey. Colonies of *Formica* were found in a variety of substrates, but 84.7% of their colonies were located under rocks, in mounds, or in soft, rotting wood, easily accessible to foraging bears. On the LaSal Mountains this genus is a widely distributed and relatively vulnerable prey to foraging black bears. In a neighboring low-elevation plateau to the north (Book Cliffs), a similar broad distribution and abundance of this genus was found (Seid 1997).

Several factors may contribute to bears' use or avoidance of certain ant genera. Redford (1987) showed that mammals that prey on ants seem to prefer subfamilies Formicinae (e.g., *Formica*, *Lasius*, and *Camponotus*) and Dolichoderinae (e.g., *Tapinoma*), both of which lack a functional sting, whereas the subfamily Myrmicinae (e.g., *Myrmica*), that possesses a functional sting, appears to be avoided. A similar pattern for neotropical anteaters (Myrmecophagidae) was noted by Montgomery and Lubin (1977). Our data support this pattern with a single exception: *Tapinoma* does not have a functional sting, and yet it was seldom eaten by black bears in our study area. *Tapinoma* adults have the smallest body size and dry weight, which may explain in part why they were less attractive to bears.

TABLE 3. Percent distribution of nest type throughout major habitat types on the LaSal Mountains, UT. Percentages of nest types within habitats sum to 100%.

		Nest type							
Habitat	# of nests	Rock	Mound	Litter	Dung	Under wood	In wood	Rotting wood	Crevice
Pinyon-Juniper	125	70.4	13.6		0.8	12.8	0.8	0.8	0.8
Ponderosa pine	132	61.4	8.3		3.0	17.4	2.3	6.8	0.8
Oak–Mountain brush	150	74.0	16.0		5.3	2.0	0.7		2.0
Aspen	152	22.4	0.7	3.3	2.0	29.6	14.5	27.6	
Spruce-Fir	81	32.1	16.1	2.5		89.6	3.7	37.0	
ALL HABITATS	640	53.1	10.3	1.1	2.5	14.7	4.7	12.8	0.8

TABLE 4. The percent distribution of nest type (location) among 18 genera of ants on the LaSal Mountains, UT. Percentages sum to 100% within rows. Note the importance of rocks and the diversity of nest types used by *Formica* and *Myrmica* ants commonly and infrequently (respectively) consumed by black bears.

Genus	Sample	Rock	Mound	Litter	Dung	Under wood	In wood	Rotting wood	Crevice
Acanthomyops	3	100.0							
Aphaenogaster	4	50.0			50.0				
Camponotus	51	74.5		2.0		5.9	11.7	5.9	
Conomyrma	2	50.0	50.0						
Crematogaster	1	100.0							
Forelius	11	36.4				54.5		9.1	
Formica	177	32.2	31.6	0.6	0.6	4.5	7.3	20.9	2.3
Lasius	155	66.5		1.9	1.9	14.9	1.9	12.9	
Leptothorax	30	20.0				23.3	16.7	40.0	
Liometopum	4	75.0				25.0			
Monomorium	11	81.8	18.2						
Myrmecocystus	1	100.0							
Myrmica	84	57.1	1.2	1.2	1.2	28.6	1.2	8.3	1.2
Pheidole	9	77.8	22.2						
Pogonomyrmex	4		100.0						
Solenopsis	16	100.0							
Stenamma	1	100.0							
Tapinoma	76	52.6		1.3	11.9	29.0	2.6	2.6	
ALL GENERA	640	53.1	10.3	1.1	2.5	14.7	4.7	12.8	0.8

TABLE 5. Ant genera found in samples of 100 black bear scats from the LaSal Mountains, UT, during 1987–1989. Only occurrences of ≥20 heads per sample for a given genus were used in computing median number of ant heads per scat.

Genus	Length (mm)	Total occurrences (≥20 heads per whole scat)	Median ant heads per scat	Maximum ant heads per scat
Formica	4.5–7.0	94	704	14,368
Lasius[a]	3.0–5.0	52	312	12,160
Tapinoma	2.0–2.5	32	116	2712
Myrmica	4.0–5.0	17	96	736
Camponotus	7.0–12.0	22	60	1568
Monomorium	1.0–1.5	2	200	240
Leptothorax	2.5–3.0	1		32
Pheidole	1.0–1.5	2	56	88
Solenopsis	1.0–1.5	0[b]		16
Aphaenogaster	4.0–4.5	5	104	400
Liometopum	3.0–4.0	1	160	160
Polygerus	6.0[c]	0[b]		8

[a]*Acanthomyops* specimens are included with *Lasius*.
[b]Found in scat, but never ≥20 heads in a whole scat.
[c]Genera not represented in our colony sampling; size from Wheeler and Wheeler (1986).

Although ant nests varied in location and potential vulnerability, 12 of 18 genera in our study area were found in bear scats. This indicates that bears were successful in finding genera that were not abundant in our colony sample. *Formica* routinely build nests that have an aboveground thatch component used as brooding chambers. Fully 31.2% of the 178 *Formica* colonies were the thatch variety. These clearly visible nests of *Formica* may increase vulnerability of the species to foraging bears, which could account in part for their frequent consumption. Additionally, *Formica* and *Myrmica* were the only genera with colonies in all 8 substrate types. While both use the same diverse nest locations, *Formica* is frequently eaten and *Myrmica* with its defensive sting is not. *Pogonomyrmex* is a semiarid genus occurring at lower elevations in our study area. Stings of these ants produce intense pain in humans and probably in bears as well. We have never observed *Pogonomyrmex* in the examination of >1700 black bear scats from Utah (Black unpublished data).

Given that 53% of all nests were found under rocks and 94% of ant genera on the LaSal Mountains use rocks as nest sites, rock-turning by black bears would seem to be the foraging strategy of choice. Odor, ant activity, and perhaps geometry of the rock (Seid 1997) are clues a bear might use to select rocks bearing ants; however, rocks are often turned and the soil beneath gives no indication that an ant colony was there. In contrast, thatch mounds are visually distinctive, and a bear with a thatch mound search image is guaranteed success when investigating *Formica* mounds, with the exception of recently vacated or dead colonies.

When eating ants, bears ingest brood as well as adult workers and alates. For example, a 41-kg, 2.5-year-old male bear shot in mid-July as a nuisance bear had consumed 2.1 kg (wet weight) of *Formica*, approximately 7840 workers and 54,700 brood (Seid 1997). The value of this meal was about 695 calories, which would have provided about 37% of this bear's daily maintenance requirement (McNab 1988, Robbins 1993). His intestines were empty, suggesting that he had obtained this meal a short time before death. The brood-to-adult ratio of the stomach contents was 7:1, far greater than the average of 2.0 ± 0.79 (s) obtained from sampling 379 colonies representing 8 ant genera in the same habitat (Seid 1997). Samples taken by Seid (1997) were from beneath rocks only. The vomitus of the bear we examined contained ants in a ratio of 3.8:1. Others have also reported that brood found in stomachs significantly outnumber adult ants (Bigelow 1922, Hatler 1972; but see Noyce et al. 1997 for an exception for the genus *Acanthomyops*).

In light of this, if a single scat represents only a portion of a meal and because several scats are produced in a 24-hour period (personal observation), then daily ant intake is greater than the analysis of an isolated scat would indicate. For comparison, the daily ant intake for the giant anteater (*Myrmecophaga tridactyla*) is 14,253 individuals (Montgomery

TABLE 6. Nutritional values (% dry mass) of the 5 ant genera most frequently found in black bear scats collected from the LaSal Mountains, UT.

Genus	Caste	Dry mass (mg)	H_2O	Crude fiber	Nitrogen (N)	Crude protein (CP)[b]	CP adjusted for chitin[c]	Fat	Ash	Carbohydrate[d]	cal · g^{-1} [e]
Formica	worker	4.3	78.6	21.5	9.5	59.4	53.9	20.3	3.4	9.6	4.9
	pupae	1.9	76.8	9.2	9.0	56.3	56.3	24.1	3.6	3.2	5.1
Lasius	worker	0.9	59.6	12.6	6.7	41.9	36.4	46.0	4.0	0.8	6.2
	pupae	0.5	72.6	9.1	8.0	50.0	50.0	31.7	5.3	0.2	5.4
Tapinoma[a]		0.4	67.8	8.7	6.8	42.5		32.9			
Myrmica[a]		1.0	73.9	10.6	9.4	58.8		24.9			
Camponotus	worker	10.9	65.3	35.7	8.0	50.0	44.5	22.0	4.4	16.3	4.9
	pupae	8.9	76.9	6.7	6.8	42.5	42.5	24.6	5.9	14.2	5.0
	larvae	2.2	69.0	2.8	6.2	38.8	38.8	9.2			

[a]Workers and pupae combined.
[b]N × 6.25.
[c](N − 0.88) 6.25 (Noyce et al. 1997, Wigglesworth 1972), except for pupae and larvae in which chitin content is negligible.
[d]100 − (% adj. CP + % chitin + % fat + % ash), % chitin equals 12.8%.
[e]4.8 (% adj. CP) + 9.5 (% fat) + 4.2 (% carbohydrate).

and Lubin 1977); for the northern tamandua (*Tamandua mexicana*), 9000; and for the silky anteater (*Cyclopes didacylus*), 700–4700 (Montgomery 1985). Brood constituted <10% of the individuals ingested by the latter 2 specialists (Montgomery 1985). Thus, black bears would appear to rival many ant specialists as ant predators (Table 5).

Seasonally, the amount of brood varies, but apparently brood is usually available regardless of season and is rather ubiquitous (Noyce et al. 1997, Swenson et al. 1999, this study). We suspect that brood extraction is a primary motivation for foraging at colonies and might explain cropping behavior common in bears and other myrmecophagous species (Noyce et al. 1997, Swenson et al. 1999). Our observations at thatch mound nests of *Formica* revealed intense nest reconstruction following bear attacks, with hundreds, if not thousands, of workers teeming over the disturbed nest. If consumption of workers is most important, bears should simply disturb a colony and wait for immediate worker recruitment to the damaged site (Hölldobler and Wilson 1990). Bears may leave nests because little or no brood was found or because available brood was consumed. In the cropping scenario many workers would be consumed incidental to the ingestion of brood. Given that some Formacine ants have low formic acid content (Swenson et al. 1999), are devoid of stings, have little armor, and exhibit little aggression when nests are disturbed, black bears should be able to feed on them with relative impunity. High brood-to-adult ratios in the stomachs of bears strongly suggest that at least on some occasions adults are not the prey being harvested.

Nutritional Considerations

Several reasons have been proposed for the inclusion of ants in diets of omnivores. They may represent a spicy snack or condiment (Nishida and Hiraiwa 1982, Dufour 1987) or supply a food high in fat and protein (McGrew 1974, Landers et al. 1979, Beeman and Pelton 1980, Nishida and Hiraiwa 1982, Maehr and Brady 1984, Dufour 1987, Redford 1987). There was no clear pattern in our data to indicate that pupae contain higher amounts of fat than workers. It has been shown, however, that ant and termite alates have relatively more fat than workers of the same species (Griffiths 1968, Redford and Dorea 1984, Dufour 1987, Noyce et al. 1997). We have no nutritional data for alates, but higher digestibility and lack of defense mechanisms of the pupae may make them more preferable to bears.

Nutritionally, *Formica, Lasius,* and *Camponotus* workers consistently had higher crude fiber than their respective pupae (Table 6). Higher crude fiber content in adults was probably due to chitin, because adult exoskeletons were not digested during fiber analysis but remained as readily identifiable pieces in the residue measured as crude fiber. Thus, eggs, pupae, and larvae, all of which lack thick chitin-containing exoskeletons, may be more digestible to bears. In some areas in North America, from spring emergence until the ripening of summer mast crops, bears gain weight slowly (Noyce and Garshelis 1998). During this time ant utilization is higher than in other seasons (Tisch 1961, Hatler 1972, Landers et al. 1979, Beeman and Pelton 1980, Maehr and Brady 1984, Rogers 1987, Raine and Kansas 1990, Noyce et al. 1997) and may be critical to growth and maintenance. The percentages of fat, carbohydrate, and protein actually available to bears from ants are not known. Brody and Pelton (1988) showed that the digestibility of gross energy and crude protein for black bears changes from summer to fall. Additionally, bears may produce elevated production of chitinolytic enzymes when consuming quantities of ants. This has been shown for some other vertebrates (Jeuniaux 1961, Cornelius et al. 1976).

Conclusions

Black bears consume a variety of ant taxa but may select those that occur at high colony densities; lack a functional sting; have low formic acid content, large body size, and large colonies; and build conspicuous nests. They may prefer ant brood over adults because brood have a lower crude fiber content and have no apparent chemical, anatomical, or behavioral defenses. Energy values of ants coupled with high-volume consumption suggest that ants provide black bears with an important source of food. This study gives additional support to the speculation of Stirling and Derocher (1990) that black bears may be facultatively, if not obligately, myrmecophagous, at least seasonally. The density, diversity, and geographic distribution of ants accommodate this trophic adaptation.

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Literature Cited

ALLRED, D.M. 1982. Ants of Utah. Great Basin Naturalist 42:415–511.

BATES, J.W., AND A. HENRY. 1999. 1998 Utah black bear harvest Publication 99-25. Utah Department of Natural Resources, Division of Wildlife Resources. Salt Lake City. 21 pp.

BEEMAN, L.E., AND M.R. PELTON. 1980. Seasonal foods and feeding ecology of black bears in the Smoky Mountains. International Conference on Bear Research and Management 4:141–147.

BIGELOW, N.K. 1922. Insect food of the black bear (*Ursus americanus*). Canadian Entomologist 43:49–50.

BRODY, A.J., AND M.R. PELTON. 1988. Seasonal changes in digestion in black bears. Canadian Journal of Zoology 66:1482–1484.

CORNELIUS, C., G. DANDRIFOSSE, AND C. JEUNIAUX. 1976. Chitinolytic enzymes of the gastric mucosa of *Perodictus potto* (Primate Prosimian): purification and enzyme specificity. International Journal of Biochemistry 7:445–448.

DUFOUR, D.L. 1987. Insects as food: a case study from the northwest Amazon. American Anthropologist 89: 383–397.

GRABER, D.M., AND M. WHITE. 1983. Black bear food habits in Yosemite National Park. International Conference on Bear Research and Management 5:1–10.

GRIFFITHS, M. 1968. Echidnas. Pergamon Press Ltd., Oxford, UK. 282 pp.

HATLER, D.F. 1972. Food habits of black bears in interior Alaska. Canadian Field-Naturalist 86:17–31.

HÖLLDOBLER, B., AND E.O. WILSON. 1990. The ants. Belknap Press of Harvard University Press, Cambridge, MA. 732 pp.

JEUNIAUX, C. 1961. Chitinase: an addition to the list of hydrolases in the digestive tract of vertebrates. Nature 192:135–136.

JOHNSON, L.A. 1996. Black bear myrmecophagy in the Central Upper Peninsula of Michigan. Master's thesis, Northern Michigan University, Marquette. 67 pp.

LANDERS, J.L., R.J. HAMILTON, A.S. JOHNSON, AND R.L. MARCHINTON. 1979. Foods and habitat of black bears in southeastern North Carolina. Journal of Wildlife Management 43:143–153.

MAEHR, D.S., AND J.R. BRADY. 1984. Food habits of Florida black bears. Journal of Wildlife Management 48: 230–235.

MATTSON, D.J. 2001. Myrmecophagy by Yellowstone grizzly bears. Canadian Journal of Zoology 79:779–793.

MCGREW, W.C. 1974. Tool use by wild chimpanzees in feeding upon drive ants. Journal of Human Evolution 3:501–508.

MCNAB, B.K. 1988. Complications inherent in scaling the basal rate of metabolism in mammals. Quarterly Review of Biology 63:25–54.

MERRIAM, C.H. 1898. Life zones and crop zones of the United States. USDA, Bureau of Biological Survey Bulletin 10:1–79, 1 map.

MONTGOMERY, G.G. 1985. Impact of vermilinguas (*Cyclopes, Tamandua:* Xenarthra = Edentata) on arboreal ant populations. Pages 351–363 *in* G.G. Montgomery, editor, The evolution and ecology of armadillos, sloths, and vermilinguas. Smithsonian Institute Press, Washington, DC.

MONTGOMERY, G.G., AND Y.D. Lubin. 1977. Prey influences on movements of neotropical anteaters. Pages 103–131 *in* R.L. Phillips and C. Jonkel, editors, Proceedings of the 1975 Predator Symposium. Montana Forest and Conservation Experiment Station, University of Montana, Missoula.

NISHIDA, T., AND M. HIRAIWA. 1982. Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. Journal of Human Evolution 11:73–99.

NOYCE, K.V., AND D.L. GARSHELIS. 1998. Spring weight changes in black bears in northcentral Minnesota: the negative foraging period revisited. Ursus 10: 521–531.

NOYCE, K.V., P.B. KANNOWSKI, AND M.R. RIGGS. 1997. Black bears as anteaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota. Canadian Journal of Zoology 75: 1671–1686.

RAINE, R.M., AND J.L. KANSAS. 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. International Conference of Bear Research and Management 8:297–304.

REDFORD, K.H. 1987. Ants and termites as food: patterns of mammalian myrmecophagy. Pages 349–399 *in* H.H. Genoways, editor, Current mammalogy. Plenum Press, New York.

REDFORD, K.H., AND J.G. DOREA. 1984. The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. Journal of Zoology 203: 385–395.

RICHARDSON, W.S. 1991. Habitat selection and feeding ecology of black bears in southeastern Utah. Master's thesis, Brigham Young University, Provo, UT. 75 pp.

RICHMOND, G.M. 1962. Quaternary stratigraphy of the LaSal Mountains. Geological Survey Professional Paper 324. United States Department of the Interior, Geological Survey. 135 pp.

ROBBINS, C.T. 1993. Wildlife feeding and nutrition. Academic Press, San Diego, CA. 352 pp.

ROGERS, L.L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monographs 97:1–72.

SEID, M.A. 1997. Ant colonies under rocks as a food source for black bears (*Ursus americanus*). Master's thesis, Brigham Young University, Provo, UT. 47 pp.

STIRLING, I., AND A.E. DEROCHER. 1990. Factors affecting the evolution and behavioral ecology of the modern bears. International Conference on Bear Research and Management 8:189–204.

SWENSON, J.E., A. JANSSON, R. RIIG, AND F. SANDEGREN. 1999. Bears and ants: myrmecophagy by brown bears in central Scandinavia. Canadian Journal of Zoology 77:551–561.

TISCH, E.L. 1961. Seasonal food habits of the black bear in the Whitefish Range of northwestern Montana. Master's thesis, Montana State University, Bozeman. 108 pp.

WHEELER, G.C., AND J.N. WHEELER. 1986. The ants of Nevada. Allen Press, Inc., Lawrence, KS. 138 pp.

WIGGLESWORTH, V.B. 1972. The principles of insect physiology. 7th edition. Chapman and Hall, London. 827 pp.

WILLIAMS, S., EDITOR. 1984. Official methods of analysis. 14th edition. Association of Official Analytical Chemists, Inc., Arlington, VA. 1141 pp.

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