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Bruce A. Kimball
United States Department of Agriculture, National Wildlife Research Center; and , Colorado State University, bruce.kimball@ars.usda.gov

Dale L. Nolte
USDA-APHIS-Wildlife Services, Dale.L.Nolte@aphis.usda.gov

Richard M. Engeman
USDA-APHIS-Wildlife Services, s_r100@yahoo.com

John J. Johnston
United States Department of Agriculture, National Wildlife Research Center

Frank R. Stermitz
Colorado State University - Fort Collins

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CHEMICALLY MEDIATED FORAGING PREFERENCE OF BLACK BEARS (*URSUS AMERICANUS*)

BRUCE A. KIMBALL, DALE L. NOLTE, RICHARD M. ENGEMAN, JOHN J. JOHNSTON, AND FRANK R. STERMITZ

United States Department of Agriculture, National Wildlife Research Center, 3350 Eastbrook Drive, Fort Collins, CO 80525; and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523 (BAK)
United States Department of Agriculture, National Wildlife Research Center, 9701 Blomberg Street SW, Olympia, WA 98512 (DLN)
United States Department of Agriculture, National Wildlife Research Center, 1716 Heath Parkway, Fort Collins, CO 80524 (RME)
United States Department of Agriculture, National Wildlife Research Center, 3350 Eastbrook Drive, Fort Collins, CO 80525 (JJJ)
Department of Chemistry, Colorado State University, Fort Collins, CO 80523 (FRS)

The role of chemical constituents in the foraging behavior of black bears (*Ursus americanus*) was investigated using two field studies. Vascular tissue samples were collected from Douglas-fir (*Pseudotsuga menziesii*) trees recently foraged by black bears. Samples were extracted and analyzed by liquid and gas chromatography to determine carbohydrates and terpenes, respectively. Chemical data were subjected to correlation analyses and multiple regression to examine if they adequately describe observed foraging preferences. Free-ranging black bears also were offered a choice of four test diets that differed in content of carbohydrates and terpenes. Results indicated that forage preferences were based in part on chemical constituents in the forage. Black bears maximized intake of carbohydrates and minimized intake of terpenes. In multiple choice tests, free-ranging bears preferred a low-terpene diet to a high-terpene diet with identical carbohydrate content. Bears also preferred a high-carbohydrate diet to a low-carbohydrate diet with identical terpene content.

Key words: *Ursus americanus,* black bear, *Pseudotsuga menziesii,* chemical cues, foraging behavior, vascular tissue

After winter dormancy, black bears (*Ursus americanus*) commonly forage on Douglas-fir (*Pseudotsuga menziesii*) in spring until more desirable forage items are available. Bears feed on Douglas-fir by removing bark with their claws and scraping vascular tissue with their incisors. An individual bear can peel trunks of 50–70 trees/day and generally targets trees from 15 to 25 years old (Schmidt and Gourley, 1992). However, bears appear to be selective in harvesting vascular tissue; not all stands are selected, and one tree in a stand may be stripped while its adjacent neighbor is ignored or minimally sampled. Bears prefer trees in thinned stands versus higher density stands (Kanaskie et al., 1990; Mason and Adams, 1989; Schmidt and Gourley, 1992), and tree-species specificity also has been observed (Barnes and Engeman, 1995).

Foraging on trees is presumed to occur primarily in spring because vascular tissue is high in carbohydrates (Radwan, 1969). Highly energetic simple sugars such as sucrose, glucose, and fructose are present. Preference for those compounds has been demonstrated in other omnivores such as laboratory rats (Jacobs et al., 1978). Thus, carbohydrates may serve as chemical cues for the energetic value of vascular tissue.

Conversely, some secondary plant me-

tabolites can serve as mammalian feeding deterrents (Bryant et al., 1991, 1992). Pine oil has been shown to effectively repel snowshoe hares (*Lepus americanus*) and voles (*Microtus townsendii*—Bell and Harestad, 1987). Reichardt et al. (1990) demonstrated the deterrent qualities of several terpene compounds in balsam poplar (*Populus balsamifera*) on snowshoe hares. The concentration of certain monoterpenes was found to be the best predictor of feeding of tassel-eared squirrels (*Sciurus aberti*) on ponderosa pine (*Pinus ponderosa*—Farentinos et al., 1981).

Our studies were conducted to determine if some chemical constituents of vascular tissue were responsible for foraging preferences of black bears. We hypothesized that black bears would exhibit a preference for carbohydrates (simple sugars) and terpenes would deter feeding.

Materials and Methods

Forage analysis study.—Stands of Douglas-fir in southwestern Washington and northwestern Oregon were monitored for bear foraging activity in spring 1994 and 1995. Six sites with significant foraging activity were located by field personnel working for landowners and state and federal agencies. Only trees with areas of removed bark and incisor marks on the remaining vascular tissue were sampled for this study. In all cases, foraging occurred on the lower 1.5 m of the tree. Trees with no evident foraging marks were not sampled because it could not be ascertained if they were encountered by a foraging bear. We relied on observations of field personnel to select sites where time elapsed from foraging to sampling was <1 week. Foraging at one site (Raspberry) occurred <24 h prior to sampling. All trees with visible signs of recent foraging activity were sampled.

We determined the surface area of bark removed, diameter at breast height (dbh), and circumference at the base for each tree. Basal surface area was calculated as the surface area of the tree from base to breast height (1.5 m). Vascular tissue was collected by removing two 40- by 10-cm patches of bark on opposite sides of the tree and scraping vascular tissue (phloem and xylem oleoresin located immediately underneath the cork cambium) into a plastic freezer bag. Samples were obtained at breast height.

The freezer bag and contents were placed immediately in liquid nitrogen for 2–5 min. After complete freezing, samples were kept on dry ice until placed in a laboratory freezer at −24°C. Samples were maintained frozen until homogenized with a mallet and divided into two portions. One portion was maintained frozen until analyzed for terpenes; the other was lyophilized and analyzed for carbohydrates. Mass of vascular tissue was determined as the mass of vascular tissue per 800-cm^2 sample area.

Terpene analyses were performed by capillary gas chromatography with mass-selective detection (Kimball et al., 1995). Each vascular tissue sample was analyzed in triplicate. Terpenes identified by their mass spectra and retention times were quantified versus external standards. Samples of vascular tissue also were analyzed by gas chromatography to characterize the isomeric composition (Fig. 1). Chromatographic analysis of terpene enantiomers was performed with a β-cyclodextrin capillary column (J&W Scientific, Folsom, CA). Enantiomers also were identified with external standards and mass spectral data.

Carbohydrate analyses were performed by extracting ca. 0.5 g of freeze-dried vascular tissue with 25 ml of 50% aqueous ethanol. Extracts were analyzed by anion-exchange chromatography with electrochemical detection (Rocklin and Pohl, 1983). The process of freeze drying combined with the use of ethanol in the extraction solvent minimized the potential for enzymatic hydrolysis of sucrose by invertase (Hendrix and Peelen, 1987). Carbohydrates were quantified versus external standards. Freeze-dried samples also were analyzed in triplicate. For quantitative analyses, coniferin and an unknown carbohydrate were quantified versus fructose and lactose, respectively.

Principle components analysis was used to identify important variables (Cooley and Lohnes, 1971), but revealed only that site-to-site variability was high. Thus, the number of chemical variables was reduced by summation and each site was considered separately for multiple regression. Appropriate terpene concentrations were summed to define the following variables: hydrocarbon monoterpenes, oxygenated monoterpenes, and sesquiterpenes. Similarly, two carbohydrate variables were defined: total carbo-

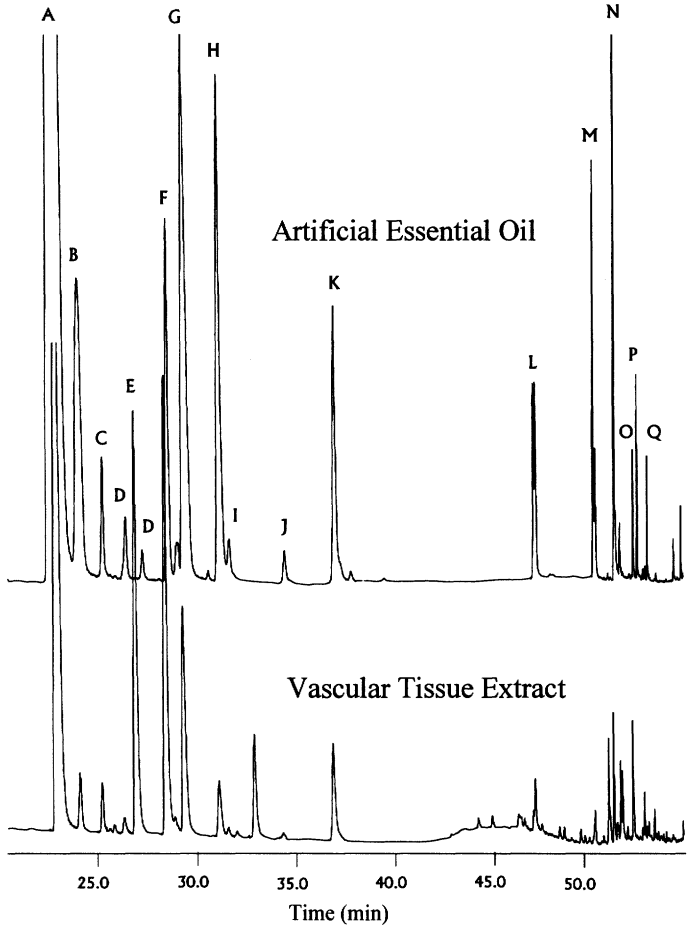

FIG. 1.—Gas chromatograms of the artificial essential oil solution and a Douglas-fir vascular tissue extract. A: (−)–α–pinene; B: (+)–α–pinene; C: myrcene; D: (±)–camphene; E: sabinene; F: (+)–3–carene; G: (−)–β–pinene; H: (−)–limonene; I: (+)–limonene; J: γ–terpinene; K: terpinolene; L: (±)–linalool; M: (−)–terpinen–4–ol; N: (−)–bornyl acetate; O: citronellyl acetate; P: (+)–longifolene; Q: caryophyllene.

hydrates and major carbohydrates (fructose, glucose, and sucrose). Concentration of the phenolic glycoside coniferin and the tree measurements dbh, basal surface area, and mass of vascular tissue also were considered as separate variables for statistical analyses. Correlational analysis was used first to assess strength of relationships among variables so that collinear variables could be removed prior to application of modeling methods. The relationship of the area of bark removed during foraging to the remaining variables was examined by multiple regression analysis. Multiple regression models were built using all remaining variables.

Field bioassay study.—Four pelleted test diets were formulated by Ferndale Grain (Ferndale, WA). The foundation of the pelletized bait consisted of 56% meat and bone meal and 43% sugar beet pulp. Sodium chloride, magnesium sulfate, and mineral vitamins for swine constituted the final 1% of the foundation. Cane sugar was added to two of the diets to increase carbohydrate concentration. The two low-carbohydrate diets relied on the sugar-beet pulp as the only source of carbohydrates.

An artificial essential oil of Douglas-fir also was added to each diet. The oil solution was prepared in the laboratory from a mixture of 17 terpene compounds (Table 1). Terpenes used and their relative concentrations were based on

TABLE 1.—*Composition of artificial Douglas-fir essential oil used to produce test diets for bioassay.*

Terpene	Percent (%)
(−) α-Pinene	61.9
(−) β-Pinene	10.7
(−) Camphene	0.7
Myrcene	2.2
(+) 3-Carene	4.2
α-Terpinene	0.2
p-Cymene	0.5
(−) Limonene	5.3
γ-Terpinene	0.2
Terpinolene	4.2
(±) Linalool	2.2
(−) Terpinen-4-ol	2.2
(−) α-Terpineol	0.3
(−) Bornyl Acetate	2.2
Citronellyl Acetate	2.2
(+) Longifolene	0.4
Caryophyllene	0.4

chemical analyses of vascular tissue of Douglas-fir from the forage-analysis study. The isomeric composition of the artificial oil closely matched the terpene composition of Douglas-fir (Fig. 1). Two compounds present in vascular tissue of Douglas-fir, sabinene and thujene, were not commercially available in necessary quantities to be incorporated into diets. The essential oil was added with vegetable oil to improve terpene homogeneity throughout each diet. In anticipation of considerable loss of volatile terpenes during diet formulation, and to ensure that high-terpene diets had significantly higher concentrations of terpenes compared with the low-terpene diets, 22 times more essential oil was added to the high-terpene diets compared with low-terpene diets (Table 2). The analytical methods used in the forage-analysis study were modified slightly for analyses of formulated diets. Five replicate samples of each diet were collected randomly and ground for analysis.

Delivery of diets was based on the supplemental feeding program of the Washington Forest Protection Association (Ziegltrum, 1994). Feeders were constructed from 55-gal drums that had an opening cut into the lower portion. Similar to many bird feeders, a metal sheet placed diagonally inside the barrel supported the bulk of the diet and allowed for continuous replacement of pellets through a narrow gap at the back of the drum. Diets were thus available at the bottom of the drum for feeding by bears. Test diets were added to the feeder through the top of the drum that was securely covered with a plywood sheet. Feeders were placed on wooden bases that kept the feeder opening ca. 35 cm off the ground. Each drum was fastened securely to a tree to prevent it from being toppled by bears. At each site, four feeders were placed 10 m from each other in a square configuration with feeder openings oriented toward a central focus.

Ten sites with a history of past bear activity were located within a 160-km radius of Olympia, Washington. Feeders were placed at each site and prebaited. The prebait treatment consisted of loading each feeder with supplemental feed used in the supplemental feeding program of the Washington Forest Protection Association and hanging a beaver carcass in a tree near feeding stations. Each site was monitored for bear

TABLE 2.—*Composition of test diets used in field bioassay study.*

Ingredient	Diet 1	Diet 2	Diet 3	Diet 4
Foundation[a] (kg)	1,690	1,815	1,690	1,815
Cane sugars (kg)	125	None	125	None
Vegetable oil (l)	19	19	19	19
Terpene solution (l)	2.2	2.2	0.1	0.1
Total terpene content (ppm)	263	290	86.1	44.9
RSD[b] (%)	(19)	(8)	(12)	(33)
Glucose content (%)	1.39	0.21	1.42	0.26
RSD	(7.2)	(3.4)	(11)	(2.7)
Sucrose content (%)	7.14	4.79	6.55	4.82
RSD	(6.0)	(7.3)	(4.9)	(5.2)

[a] Foundation: 56% Mean and bone meal, 43% Sugar beet pulp, and 1% Vitamins and minerals.
[b] Relative standard deviation.

activity every third or fourth day and feed intake was recorded.

Intake was measured by refilling the feeder from a tared bag of pelleted feed to a known reference point marked on the inside of the feeder drum. The change in mass of the bag was used as the amount consumed from that feeder. Spilled feed was replaced into the feeder prior to addition of new feed. Occasionally, spilled feed was damp and no longer in pellet form. In these instances, the mass of the wet feed was recorded. To estimate dry mass of wet feed, a brief experiment was conducted in triplicate. Known masses of feed were placed in a controlled environment and wetted three times daily for 3 days. Eight different masses ranging from 4.5 to 70 kg were used. Wet mass was regressed against dry mass, and the regression was used to estimate dry masses of spilled feeds.

Following 2 weeks of feeding activity at a site, supplemental feed was removed from each feeder, and the four test diets were placed randomly in feeders. Sites were monitored every 3–4 days for 7 monitoring periods. Intake was measured and mean daily intake was calculated for each period. Two of the 10 sites were inactive.

This was a factorial experiment where sites were blocked, and the three factors were: carbohydrate content (high and low), terpene content (high and low), and sampling period (Ott, 1993). The response was mean daily intake. Two linear contrasts were performed to test if diet intake was reduced because of increased terpene concentration at the high-carbohydrate level and if intake was increased as a result of increased carbohydrate concentration at the high-terpene level.

Results

Forage analysis study.—Vascular tissue samples of Douglas-fir were analyzed for 20 different terpenes. Typically, the most prevalent terpene compounds in order of abundance were: α-pinene, β-pinene, sabinene, limonene, 3-carene, myrcene, camphene, terpinolene, and bornyl acetate. The concentration of α-pinene was ca. 10 times that of the other major terpenes. Galactose, glucose, xylose, fructose, sucrose, coniferin, and an unknown compound were present in all extracts analyzed for carbohydrates.

Vascular tissue of Douglas-fir contained predominately one of the potential optical isomers of chiral terpenes. Through the use of known standards and spectroscopic data, α-pinene, sabinene, β-pinene, limonene, terpinen-4-ol, α-terpineol, and bornyl acetate were found in vascular tissue as (−) enantiomers. Relatively small amounts of the (+) isomers of α-pinene and β-pinene also were observed. Enantiomers of 3-carene and longifolene were identified as the (+) form. Because an optically pure standard of camphene could not be obtained, we could not distinguish which isomer was present in vascular tissue, but only one was present.

Correlation analysis identified basal surface area to be collinear with dbh, and the total carbohydrate variable was dominated by the major carbohydrate variable. Remaining variables after exclusion of basal surface area and total carbohydrates were: concentration of hydrocarbon monoterpenes, concentration of oxygenated monoterpenes, concentration of sesquiterpenes, concentration of major carbohydrates, concentration of coniferin, mass of vascular tissue, and dbh. Multiple regression yielded significant ($P \leq 0.06$) models for four of the six sites (Table 3). Coefficients of determination (R^2) from the models indicated that these variables account for 50–75% of the variation in the characteristics of removed bark. Diagnostic evaluation of multiple regression data detected no violations of the assumptions of regression analyses.

Field bioassay study.—Analyses of test diets revealed that the high-carbohydrate diets (diets 1 and 3) contained ca. 8% major carbohydrates. Low-carbohydrate diets (diets 2 and 4) contained ca. 5% carbohydrates (Table 2). Sucrose made up the majority of the carbohydrate content. Total terpene content of the high-terpene diets (diets 1 and 2) was ca. 275 μg/g. Diets 3 and 4 (low-terpene diets) had a total terpene concentration of 86 and 45 μg/g, respectively. Chem-

TABLE 3.—*Statistics from multiple regression analyses where area of removed bark was the response and the predictors were the chemical concentrations of hydrocarbon monoterpenes, oxygenated monoterpenes, sesquiterpenes, carbohydrates, and coniferin, tree diameter (dbh), and mass of vascular tissue.*

Statistics	Site					
	McCleary	Kelso	Cowlitz	Raspberry	Silver Falls	Molalla
P	0.8	0.05	0.06	0.04	0.6	0.03
R^2	0.14	0.44	0.78	0.63	0.44	0.55

ical analyses also demonstrated low variability among the five replicates (Table 2). Terpene variability was <20% (relative standard deviation, RSD—Miller and Miller, 1988) for high-terpene diets; low-terpene diets had more variation. The RSD for diet 3 was 12%; diet 4 RSD was 33%. Diets had less variation in carbohydrate concentration, from a low RSD of 2.7% for glucose content of diet 4 to a high RSD of 11% for the glucose content of diet 2.

A significant model ($P < 0.0001$) resulted from the analysis (Fig. 2). Carbohydrates had a positive effect on mean daily intake ($P < 0.0001$), but intake was decreased by terpenes ($P = 0.011$). Effects due to sampling period ($P = 0.73$), period × carbohydrate ($P = 0.72$), period × terpene ($P = 0.72$), and period × carbohydrate × terpene ($P = 0.80$) were not significant. Similarly, there was no significant carbohydrate × terpene interaction ($P = 0.12$). Results of the a priori linear comparisons demonstrated that terpenes had a deterrent effect at the high-carbohydrate level ($P = 0.006$). Furthermore, preference for carbohydrates was observed at the high-terpene level ($P < 0.0001$).

DISCUSSION

Trees with minimal (ca. 20 cm^2) bark removed during foraging frequently were found adjacent to trees with extensive (≤15,500 cm^2) bark damage. The area of removed bark was the only quantitative evidence of preference remaining after the foraging event. Thus, we assumed that trees of poor forage quality were those with min-

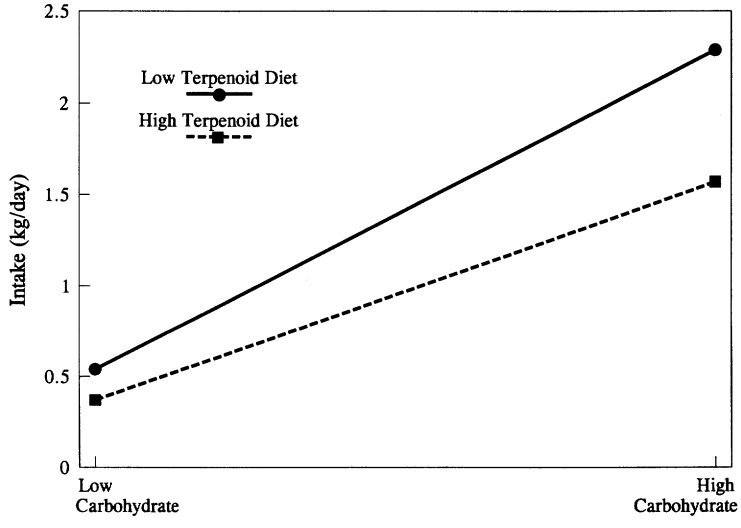

FIG. 2.—Profile plot of mean daily intake of four diets varying in concentration of carbohydrates and terpenes.

imal bark damage. Conversely, highly preferred trees were those with extensive bark removal. Our multiple-regression data indicate that chemical constituents may affect preference (Table 3), but the correlative nature of this study did not establish that the chemical constituents were related causally to preference. The field-bioassay study was designed specifically to establish causative effects on foraging preference due to carbohydrates and terpenes.

Results of the field bioassay demonstrate regulation of carbohydrate and terpene intake by a foraging mammal. Free-ranging bears in our study preferred the low-terpene diets to the high-terpene diets at the high-carbohydrate concentration. Bears also preferred the high-carbohydrate : high-terpene diet to the low-carbohydrate : high-terpene diet. This may be reflective of the energy content of the high-carbohydrate diet exceeding deleterious effects of terpenes.

Terpene avoidance initially was thought to be mediated by digestive inhibition (Connolly et al., 1980; Oh et al., 1970). This assertion was refuted by Welch and coworkers who demonstrated that the monoterpenes of sagebrush (*Artemisia*) did not impact ruminant digestibility (Welch and Pederson, 1981; Welch et al., 1983). Furthermore, Bryant et al. (1991) concluded that terpene avoidance in a monogastric species was mediated by a toxic response. It is now recognized that though secondary plant metabolites are detoxified, they have significant effects on herbivore metabolism (Foley and McArthur, 1994).

Mammalian detoxification of secondary plant metabolites involves three steps: primary metabolism, conjugation, and elimination. Secondary metabolites such as terpenes are transformed into more polar compounds by primary metabolism and conjugation. These transformation products are themselves considered a metabolically produced organic acid load (Foley et al., 1995). Because maintenance of acid-base balance is of primary importance, bicarbonate must be produced to neutralize these organic acids and associated protons at a cost of increased protein catabolism. A major consequence of the disruption of acid-base homeostasis is acidemia (Foley et al., 1995). Furthermore, depletion of glucose and amino acids for the production of glucuronic acid are direct consequences of the conjugation process (Illius and Jessop, 1995). It has been estimated that the protein cost to maintain glucuronic acid for conjugation far exceeds that of maintaining acid-base homeostasis.

Depletion of the glucose pool comes at the expense of daily energy requirements. Therefore, maximizing carbohydrate intake is not only important for maintaining basal metabolism but also for supplying substrates for terpene conjugation. In addition to malaise resulting from detoxification of ingested terpenes, it recently has been reported that monoterpenes inhibit acetylcholinesterase activity in mammals (Miyazawa et al., 1997).

It may be imperative that a foraging mammal recognize deleterious compounds before ingesting toxic levels (Levin, 1976). Affective learning processes allow foraging animals to associate taste or flavor of a diet with the post-ingestive feedbacks (Provenza et al., 1992). Terpenes taste bitter to humans, but bitterness is not necessarily indicative of toxicity (Glendinning, 1994). In fact, bitterness per se may not be responsible for terpene avoidance (Nolte et al., 1994). The flavor of terpenes (bitter or otherwise) likely was associated with effects of terpene ingestion through affective processes.

Forage preference need not necessarily be based on taste hedonics. The process of forage selection of vascular tissue by black bears may involve other sensory cues (e.g., olfactory and tactile) for initial tree selection followed by gustatory and olfactory (flavor) cues. Trees sampled in our forage-analysis study may have been preferred trees from initial sensory screening. The volatile nature of terpenes makes them ideal olfactory cues. Furthermore, olfactory rec-

ognition of vascular tissue may not be limited necessarily to terpenes. Non-taste recognition of sucrose has been reported in laboratory rats (Rhinehart-Doty et al., 1994).

Preferences for carbohydrates similarly are mediated by flavor and associated positive feedbacks of ingestion. Regulation of carbohydrate intake has been demonstrated in other omnivores (Spector and Smith, 1984). Thus, forage preferences frequently are explained by the energetic value of the forage (Sclafani, 1990). Observed preferences of isocaloric solutions also can be related to post-ingestive feedbacks. Preference for glucose over fructose may be explained in part by the faster physiological absorption rate of glucose (Ackroff and Sclafani, 1991). These differences cause post-ingestive feedbacks of glucose to be more reinforcing than feedbacks of fructose.

Foraging preferences arise from interplay between taste and feedback (Provenza, 1996). Nutrients such as carbohydrates produce positive feedbacks while toxins such as terpenes produce negative feedbacks. Foraging preferences of black bears observed in our studies may have resulted from affective learning processes. That is, taste of forage was fateful to positive and negative feedbacks of ingestion. Black bears selectively foraged in a manner that maximized energy intake and minimized intake of terpenes. Preference for forage higher in carbohydrates will be explicit as long as energetic benefits exceed cost of terpene detoxification.

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