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Terpenes May Serve as Feeding Deterrents and Foraging Cues for Mammalian Herbivores

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Abstract

Terpenes, volatile plant secondary compounds produced by woody plants, have historically been thought to act as feeding deterrents for mammalian herbivores. However, three species of woodrats, *Neotoma stephensi, N. lepida,* and *N. albigula,* regularly consume juniper, which is high in terpenes, and *N. stephensi* and *N. lepida* are considered juniper specialists. By investigating the terpene profiles in *Juniperus monosperma* and *J. osteosperma,* which are browsed or avoided by woodrats in the field, and recording the caching and consumption of juniper foliage by woodrats in the lab, we have evidence that terpenes may serve as feeding and/or foraging cues. The obligate specialist *N. stephensi* chose to forage on trees higher in p-cymene and preferred to consume juniper rather than caching it in a laboratory setting. These observations provide evidence that terpenes serve as a feeding cue and that the obligate specialist's physiological mechanism for metabolizing the terpenes present in juniper may negate the need for caching. The facultative specialist *N. lepida* chose to forage on trees lower in four terpenes and cached more juniper than the obligate specialist *N. stephensi*, providing evidence that terpenes serve as a feeding deterrent for *N. lepida* and that this woodrat species relies on behavioral mechanisms to minimize terpene intake. The generalist *N. albigula* foraged on trees with higher terpenes levels but consumed the least amount of juniper in the lab and preferred to cache juniper rather than consume it, evidence that terpenes act as foraging but not feeding cues in the generalist. Our findings suggest that volatile plant secondary compounds can act as feeding and/or foraging cues and not just feeding deterrents in mammalian herbivores.

Keywords Plant-mammal interactions · Terpenes · *Neotoma* · Herbivory · Dietary specialization

Introduction

Plant-mammal interactions are mitigated by the secondary compounds (PSC) produced by plants. One of the major proposed roles of PSCs in plant-mammal interactions is to deter herbivory (Bryant et al. 1992a; Iason 2005; Palo and Robbins 1991). Despite myriad negative effects of PSCs, there are mammalian herbivores that have behavioral and or physiological mechanisms allowing them to specialize on plants that are high in PSCs (Dearing et al. 2000; Freeland and Janzen 1974; Marsh et al. 2006). For a mammalian species that has mechanisms to deal with PSCs present in their host plant, it is possible that the PSCs serve as foraging cues rather than deterrents.

Mammals use sight, smell and taste for feeding cues. While some classes of PSCs would be visible to foraging mammals, such as anthocyanins that cause color changes in ripening fruit, most PSCs are likely detected by mammals via smell or taste (Lev-Yadun and Gould 2008). Phenolics are a major class of PSCs that alter taste of plants and are known to affect palatability (Haslam 1989; Bryant et al. 1992a, b). While the role of volatile organic compounds (VOCs) in foraging behavior of phytophagous insects has been well studied (Bruce et al. 2005; Visser 1986), less is known about the role of PSC odor in the foraging behavior of mammals. Recent studies have shown that browsers such as swamp wallabies and elephants use the odor of volatile PSCs as foraging cues (Bedoya-Pérez et al. 2014; Schmitt et al. 2018; Stutz et al. 2016). Beyond these few reports, studies on the role of VOCs in the foraging behavior of mammalian herbivores are lacking, particularly for dietary specialists.

We utilized the relationship between three species of woodrats (*Neotoma*) and juniper (*Juniperus*) in the western

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USA to determine if VOCs serve as a deterrent or feeding cue for an obligate dietary specialist, a facultative dietary specialist and a dietary generalist (Shipley et al. 2009). The relationship between woodrats and juniper makes an ideal study system to investigate the role of VOCs in the foraging behavior of mammalian herbivores for a number of reasons. One is that the major class of PSCs produced by juniper are terpenes. Terpenes are neurotoxic, hepatoxic and nephrotoxic and known to act as feeding deterrents (Savolainen and Pfaffli 1978; Sperling et al. 1967; Sperling 1969; Theis and Lerdau 2003). Terpenes are also highly volatile and therefore can be classified as VOCs and serve as olfactory cues. In addition, the physiological reaction of woodrats to terpenes present in juniper has been well studied. Exposure and consumption of juniper alters detoxification enzyme expression in the nasal epithelium, liver and kidneys of woodrats, and alters gut microflora (Haley et al. 2007; Kohl et al. 2014; Magnanou et al. 2009; Skopec et al. 2007, 2013a, b; Skopec and Dearing 2011). Furthermore, we know that woodrats alter feeding and caching behavior when presented with feed containing terpenes (Torregrossa and Dearing 2009a, b; Torregrossa et al. 2011).

There are three species of woodrats that regularly consume juniper. *Neotoma stephensi* is an obligate specialist on *Juniperus monosperma* (Skopec et al. 2015). It has a range that is restricted to that of *J. monosperma* and it utilizes *J. monosperma* for 60–90% of its diet (Dial 1988; Vaughan and Czaplewski 1985). *Neotoma stephensi* has highly efficient detoxification pathways to metabolize juniper (Haley et al. 2007; Skopec et al. 2007; Skopec and Dearing 2011; Sorensen et al. 2004a, b), so we would expect that *N. stephensi* is more likely to use terpenes as feeding cues than deterrents. *Neotoma lepida* is considered a facultative specialist because it only specializes on *J. osteosperma* in part of its range (Skopec et al. 2015). When *N. lepida* co-occurs with *J. osteosperma,* it's diet can consist of up to 90% juniper, but in other parts of its range *N. lepida* consumes other plants that do not produce high levels of terpenes such as cactus, creosote, and mesquite (Brown et al. 1972; Cameron and Rainey 1972; MacMillen 1964; Smith et al. 2014). As a facultative specialist, *N. lepida* may have relatively unspecialized and inefficient detoxification pathways for terpenes. This woodrat may rely on behavioral mechanisms such as foraging on low-terpene plants, or utilizing caching to allow terpenes to volatilize before consumption, and may treat terpenes as a feeding deterrent (Magnanou et al. 2009; Torregrossa and Dearing 2009a, b). *Neotoma albigula* is a generalist and can only utilize *J. osteosperma* or *J. monosperma* as 30–50% of its diet, likely due to its inefficient detoxification of terpenes (Haley et al. 2007; Skopec et al. 2007; Sorensen et al. 2004b; Vaughan and Czaplewski 1985). Like *N. lepida*, *N. albigula* probably relies on behavioral modifications such as altering feeding behaviors and caching behaviors to avoid excess consumption of terpenes (Torregrossa and Dearing 2009b; Torregrossa et al. 2011).

In two previous studies we analyzed the terpene profiles of *J. monosperma* and *J. osteosperma* individuals that were either browsed or not-browsed by *N. stephensi* and *N. lepida,* respectively. We found that the only difference between browsed and not-browsed trees in the area occupied by *N. stephensi* was that browsed trees were higher in p-cymene (Adams et al. 2014a), while in the area occupied by *N. lepida*, browsed trees were higher in alpha-pinene but lower in alpha-campholenal, sabina ketone, and terpine-4-0 p-mentha-1, 4-dien-7-ol (Adams et al. 2016). Our results suggest that terpenes are a feeding cue for the obligate specialist *N. stephensi,* which forages on plants higher in p-cymene, and terpenes are a feeding deterrent for the facultative specialist *N. lepida,* which forages on plants that were lower in five different terpenes. We proposed to extend these observations by establishing the terpene profiles of juniper browsed and not-browsed by the generalist *N. albigula* and investigating the caching and consumption behavior of juniper in all three woodrat species in a laboratory environment. We predicted that *N. albigula* would be most sensitive to PSCs and would choose to browse on juniper that is lower in terpenes. We also predicted that the obligate specialist *N. stephensi* would need to rely the least on caching and would therefore consume the most juniper in a lab setting, while the facultative specialist *N. lepida* and generalist *N. albigula* would rely more heavily on caching juniper.

Methods and Materials

Juniper Sample Collection Woodrats characteristically browse by clipping branches at a 45° angle, facilitating the identification of browsed versus not-browsed junipers. Samples of *J. osteosperma* were collected near Castle Valley, Utah (38° 37.887' N 109° 22.038' W, 1590 m). Castle Valley, Utah is a Great Basin shrub steppe ecosystem with an average annual temperature of 12.5 °C and average precipitation of 270 mm. Utah juniper is the dominant tree species while prickly pear cactus (*Opuntia spp.)*, rabbitbrush (*Chrysothamnus spp.*), saltbrushes (*Artiplex spp.*) and sagebrush (*Artemisia*) are also common. A 0.54-km^2 area known to have a high abundance of woodrat was searched for active middens. Ten junipers with middens and evidence of foraging and were targeted for sampling similar to Adams et al. (2014a, 2016). For each browsed tree, a nearby not-browsed control was identified by the absence of a midden and no evidence of woodrat browsing. Approximately 500 g of foliage was clipped from a minimum of 10 different branches from each juniper ($n = 10$ browsed, $n = 8$ not-browsed). Foliage samples were collected on 19 February 2017, immediately placed on dry ice and kept frozen at −20 °C until 29 March 2018, when they were distilled as

described below. Herbarium vouchers were deposited in the herbarium, Baylor University, Waco Texas with the following accession numbers (BAYLU Lab Acc. *Adams15347–15,356* for browsed juniper samples and Lab Acc. *Adams15357–15,364* for not-browsed juniper samples).

Essential Oils Analysis A portion (200 g) of the thawed foliage was kept cool (20 °C) and in the dark before exhaustively steam-distilled for 3 h using a modified circulatory Clevenger-type apparatus (Adams 1991). Oil samples were concentrated (diethyl ether trap-removed) with nitrogen, weighed, and stored at −20 °C until analyzed. Steam distilled leaves were oven dried for 48 h at 100 °C to a constant weight to determine dry matter content (DM). The mg/g DM total essential oil yield was calculated as [mass of oil extracted (mg)/mass of oil extracted (g) + DM of extracted leaves (g)].

The extracted essential oils were analyzed by GC-MS with a Hewlett-Packard (HP) 5890 GC equipped with a J & W DB-5, 0.26 mm × 30 m, 0.25-μm coating thickness, fused silica capillary column and directly coupled to an HP 5971 Mass Selective Detector (MSD). A 0.2ul aliquot of an extracted oil/diethyl ether solution (1:9) was injected, and split 1:10. The temperature program was a linear gradient from 60 °C to 246 °C at 3 °C/min over 62 min. The carrier gas was helium with a flow of 34.96 cm/s or 1.02 ml/min. The injector was set to 220 °C and the detector was set to 240 °C, with a scan time of 1/s(see Adams 2007, p. 4, for detailed operating conditions). Identifications were made by searches of our volatile oil library (Adams 2007) using HP ChemStation library search routines, coupled with retention time data of authentic reference compounds (see www.juniperus.org for a pdf containing the sources of each of the 2205 compounds in: The Identification of essential oil components by gas chromatography/ mass spectrometry, 4th ed., Adams 2007).

Quantification of individual compounds was by flame ionization detector (FID) on an HP 5890 gas chromatograph operated under the same conditions as the GCMS (above) using the HP ChemStation software. FID ion counts were normalized by total ions to obtain the percent concentrations for individual peaks (components), utilizing equal ion response factors for all components because individual ion response correction factors are not available for most of these terpenes. The data were reported as % of total oil for each identified terpene. The % of total oil was converted to mg/g DM for each compound using the mass-based total essential oil yield for browsed or not-browsed plants: [(% of total oil yield for each terpene/100) X total essential oil yield (mg/g DM extracted leaves)].

Protein-Precipitable Phenolics (PPP) Protein-precipitable phenolics (PPP) were measured according to Hagerman and Butler's (1978) scaled-down method as modified to determine protein precipitability of condensed tannins in two duplicate crude plant extracts (Naumann et al. 2013). Dried (55 °C) and ground (2-mm screen) 50-mg plant samples were extracted in a 50:50 methanol solution for 30 min before analysis as described Naumann et al. (2013). The absorbances were compared to a standard curve created with purified tannins isolated from dried *J. osteosperma* leaves via the method described by Wolfe et al. (2008) using Sephadex LH-20 (GE Healthcare Bio-Sciences Corp., Piscataway, NJ, USA).

Crude Protein Concentration Dried (55 °C) and ground (2-mm screen) 200-mg plant sub-samples samples were assayed for nitrogen (N) concentration by combustion using an Elementar vario Macro C:N analyzer (Elementar Americas, Inc., Mt. Laurel, NJ, USA). This system combusts plant material at high temperature and provides total N content readings. Crude protein concentration was calculated by multiplying N concentration by 6.25.

Animals *Neotoma stephensi* (8 females, 5 males) were trapped outside of the Wupatki National Monument in Woodhouse Mesa, Arizona (35°30' N, 111°27' W). *Neotoma lepida* (4 females, 4 males) were trapped near White Rocks in Tooele County, Utah (40°19'N, 112°54'W). *Neotoma albigula,* (5 females, 5 males) were collected in Castle Valley, Utah (38°30′N, 109°18′W). All three species were transported to the Weber State University Animal Facility in Ogden, Utah. When not in an experiment, woodrats were housed in individual cages (48 × 27 × 20 cm) with aspen pine shavings (Harlan Teklad). Each individual cage was connected to the Techniplast Smart Flow Air Handling Unit (TSFAHU). Environmental conditions were 12:12-h light: dark cycle, with temperatures ranging from 20 to 25 °C. The woodrats were fed standard rabbit chow (Harlan Teklad formula 2031), distilled water, and small apple slices ad libitum. All experimental procedures regarding woodrats were approved by Weber State University's Institutional Animal Care and Use Committee protocol number 11–02 and followed American Society of Mammologist guidelines (Sikes and Gannon 2011).

Caching Trials Animals had 15 g of thawed juniper foliage (*J. monosperma* for *N. stephensi* and *J. osteosperma* for *N. lepida* and *N. albigula*) added to their cages daily for 7 d prior to the caching trials. This exposure was necessary since it takes a minimum of 3 d for animals to upregulate the detoxification enzymes necessary to consume juniper (Skopec et al. 2007). The *J. monosperma* was collected at Wupatki National monument when *N. stephensi* were trapped (March 2017) and *J. osteosperma* was collected from Castle Valley when the *N. albigula* were trapped (February 2017). Collected juniper foliage was kept at −20 °C until used for caching trials. For the three-day caching trials animals were weighed and placed in polycarbonate shoebox cages (48 × 27 × 20 cm) that had feeder hoods (8 × 9 × 13 cm) attached at opposite ends of the cage.

On a daily basis, woodrats were offered 15 g of rabbit chow in one feeder hood, while the other feeder hood contained 15 g of juniper. Food was considered cached when an animal removed it from the feeder hood and placed it in their cage. Cached food within woodrat cages was removed and weighed on a daily basis. Food consumption and body mass were also measured on a daily basis. Food consumption was calculated as the difference between the amount of food provided each day and the sum of the amount of food cached and the amount of food remaining in the feeder hood. For each day of the trial, all cached items were removed from the cage, separated, and weighed and each feeder hood was replenished with 15 g of rabbit chow or juniper. We have not seen any evidence that cache removal alters woodrat caching behavior, consistent with other wild rodents in which caching is a fixed response (Luo et al. 2014). At the end of the three-day trial, woodrats were placed back into their home cages. The proportion of items cached or consumed by each animal was calculated as the weight of items cached or consumed divided by the weight of items provided. The proportion of items cached or consumed by each animal was averaged within each 3-day trial.

Statistical Analysis Total essential oil yields (as mg/g DM), individual terpenes (as % of total oil and as mg/g DM), PPP, and N concentrations were compared between browsed and not-browsed samples by analysis of variance (ANOVA) and Student-Newman-Keuls analyses as described by Steele and Torrie (1960) in JMP 12. Pearson correlations were used to determine if there were correlations between total essential oil yields as mg/g DM, crude protein levels as % of DM, and PPP as mg/g DM levels in browsed and not-browsed juniper foliage (JMP 12).

The proportion of items cached and consumed were arcsine square root transformed and compared between species using analysis of covariance with species and item (rabbit chow or juniper) as the independent variables and body mass as the covariate. Post hoc Tukey's honest significance difference (HSD) were used to test pairwise comparisons between means (JMP 12). Differences were considered significant at $P \leq 0.05$.

Results

Terpene, Tannin, and Nutrient Profiles of Browsed Versus Not-Browsed Trees Browsed trees had higher total essential oil yields (10.54 mg/g DM) compared to not-browsed trees (7.61 mg/g DM) (*F ratio 4.65, p < 0.05*). A detailed compositional analysis of *J. osteosperma* volatile leaf oils in *N. albigula's* range from browsed and not-browsed trees is shown in Table 1. On the basis of % total essential oil, α-pinene was higher in browsed than not-browsed trees, whereas sabina ketone was lower in browsed trees (Table 2). On a mg/g DM basis, four compounds were greater in browsed trees: α-pinene, β-phellandrene, terpinolene, and verbenone. Only one compound, sabina ketone, was lower in browsed trees on a mg/g DM basis (Table 2). Analyses of PPP and crude protein concentrations revealed no differences in leaves from browsed and not-browsed trees (Table 3).

An analysis of correlation among total essential oil yields (mg oil/g DM), protein content, and PPP for browsed and not-browsed trees (Table 3) revealed no correlations. However, a negative correlation was found between PPP and protein content in the not-browsed trees (Table 3).

Caching Trials There were species differences in the caching behavior of both rabbit chow ($F_{2,27} = 8.52$ $P = 0.0014$) and juniper ($F_{2,27} = 18.63$, $P < 0.001$) with *N. albigula* caching more rabbit chow than the two specialists and *N. stephensi* caching less juniper than *N. albigula* and *N. lepida* (Fig. 1). All three species preferred to cache juniper over rabbit chow (Tukey HSD $P < 0.05$). There were also species differences in how much juniper was consumed ($F_{2,27} = 3.94$ $P = 0.03$) with *N. stephensi* consuming more juniper than *N. albigula*. There was a trend for *N. stephensi* to consume less rabbit chow than the other species ($F_{2,27} = 3.07$ $P = 0.063$). Both *N. albigula* and *N. lepida* consumed more rabbit chow than juniper (Tukey HSD $P < 0.05$), while *N. stephensi* did not show a preference (Tukey HSD $P > 0.05$).

Discussion

Plant secondary compounds are broadly thought to be feeding deterrents for mammalian herbivores; however, a number of mammalian species have behavioral and/or physiological mechanisms to overcome the toxic effects of PSCs and are dietary specialists on phytochemically complex plants like juniper (Freeland and Janzen 1974; Iason 2005). By comparing the foraging behavior of three species of woodrats that vary in their degree of specialization on juniper, from the obligate specialist *N. stephensi*, to the facultative specialist *N. lepida,* and the generalist *N. albigula,* we show that each species responds differently to juniper. Our data suggest that *N. stephensi* likely uses terpenes as feeding cues, while *N. lepida* is likely deterred by terpenes and *N. albigula* likely uses terpenes as foraging cues but feeding deterrents (Table 4).

Obligate specialists, such as *N. stephensi,* have a narrow dietary and habitat niche and have likely evolved highly efficient mechanisms for dealing with large doses of a limited range of PSCs (Freeland and Janzen 1974; Shipley et al. 2009). In a previous study we found that *N. stephensi* chose to forage on juniper trees that had high levels of p-cymene, suggesting that terpenes may be feeding cues for this obligate specialist (Adams et al. 2014a). In the present caching and foraging experiment, *N. stephensi* cached less juniper and consumed more juniper than the other two species. *Neotoma*

Table 1 Leaf essential oil compositions (% total oil basis and mg/g DM basis) for *J. osteosperma* from trees browsed and not-browsed by *N. albigula*

		Browsed trees	Not-browsed	*F* ratio	Browed trees	Not-browsed	*F* ratio
	Essential oil yields	**1.05%**	**0.76%**	**4.594*[d]**	**10.54 mg**	**7.61 mg**	**4.65 ***
KI[a]	Compounds[b]	% total oil[c]	% total oil	*F*-ratio	mg/g DM[d]	mg/g DM	*F*-ratio
846	(2*E*)-hexenal	t[e]	t	nt[f]	t	t	nt
921	tricyclene	0.2	0.3	nt	t	t	nt
924	α-thujene	t	0.1	nt	t	t	nt
932	**α-pinene**	**2.32**	**1.32**	**5.59***	**0.23**	**0.10**	**13.69 ****
946	camphene	0.2	0.3	nt	t	t	nt
953	thuja-2,4-diene	0.1	0.1	nt	t	t	nt
969	sabinene	0.93	2.28	0.833 ns	0.31	0.24	0.47 ns
974	β-pinene	t	t	nt	t	t	nt
988	myrcene	0.57	0.49	0.414 ns	0.06	0.04	3.02 ns
1002	α-phellandrene	t	0.1	nt	t	t	nt
1014	α-terpinene	0.55	0.50	0.367 ns	0.05	0.04	1.96 ns
1020	p-cymene	1.97	1.65	0.276 ns	0.17	0.13	0.88 ns
1024	limonene	1.36	1.26	0.238 ns	0.14	0.10	2.36 ns
1025	**β-phellandrene**	1.10	0.75	4.03 ns	**0.11**	**0.07**	**4.88 ***
1044	(*E*)-β-ocimene	t	t	nt	t	t	nt
1054	γ-terpinene	1.08	1.06	0.010 ns	0.11	0.08	2.24 ns
1065	cis-sabinene hydrate	0.93	0.93	0.001 ns	0.10	0.07	2.09 ns
1067	cis-linalool oxide	t	t	nt	t	t	nt
1078	camphenilone	t	t	nt	t	t	nt
1086	**terpinolene**	0.72	0.65	0.364 ns	**0.07**	**0.05**	**4.69 ***
1098	trans-sabinene hydrate	1.46	1.54	0.072 ns	0.16	0.11	1.39 ns
1102	isopentyl-isovalerate	t	t	nt	t	t	nt
1112	3-me-3-buten-me-butanoate	t	t	nt	t	t	nt
1118	cis-p-menth-2-en-1-ol	t	t	nt	T	t	nt
1122	α-campholenal	1.45	1.43	0.009 ns	0.14	0.11	2.52 ns
1141	camphor	22.99	21.74	0.103 ns	2.60	1.63	2.11 ns
1141	verbenol	11.50	10.94	0.080 ns	1.28	0.82	1.83 ns
1145	camphene hydrate	1.70	1.59	0.243 ns	0.19	0.12	3.21 ns
1154	**sabina ketone**	**0.95**	**1.25**	**4.429 ***	0.10	0.10	0.00 ns
1160	pinocarvone	0.2	0.2	nt	t	t	nt
1165	borneol	6.30	8.19	1.272 ns	0.68	0.64	0.04 ns
1174	terpinen-4-ol	7.91	7.66	0.029 ns	0.76	0.58	2.30 ns
1179	p-cymen-8-ol	1.00	1.14	0.384 ns	0.10	0.09	0.14 ns
1186	α-terpineol	0.73	0.73	0.001 ns	0.07	0.05	1.58 ns
1195	myrtenol	0.6	0.9	nt	t	t	nt
1204	**verbenone**	2.46	2.00	0.710 ns	**0.23**	**0.15**	**4.57 ***
1215	trans-carveol	2.39	2.25	0.103 ns	0.23	0.17	2.90 ns
1219	coahuilensol, me-ether	t	t	nt	t	t	nt
1223	citronellol	t	t	nt	t	t	nt
1226	cis-carveol	0.4	0.3	nt	t	t	nt
1238	cumin aldehyde	0.3	0.5	nt	t	t	nt
1239	carvone	0.99	1.16	3.617 ns	0.10	0.09	0.49 ns
1283	α-terpinen-7-al	t	t	nt	t	t	nt
1284	bornyl acetate	10.82	12.55	0.283 ns	1.18	0.98	0.26 ns
1298	carvacrol	0.4	0.9	nt	t	t	nt
1320	thymol, me ester,isomer	0.48	0.50	0.027 ns	0.05	0.04	0.47 ns

Table 1 (continued)

		Browsed trees	Not-browsed	*F* ratio	Browed trees	Not-browsed	*F* ratio
1325	p-mentha-1,4-dien-7-ol	0.80	0.95	0.697 ns	0.08	0.07	0.31 ns
1468	pinchotene acetate	0.2	0.2	nt	t	t	nt
1513	γ-cadinene	t	t	nt	t	t	nt
1522	δ-cadinene	t	t	nt	t	t	nt
KI[a]	yields/ Compounds[b]	Browsed trees % total oil	Not-browsed % total oil	*F* ratio	Browed trees mg/g DM	Not-browsed mg/g DM	*F* ratio
1548	elemol	1.65	1.25	1.833 ns	0.17	0.09	3.58 ns
1574	germacrene-D-4-ol	t	t	nt	t	t	nt
1582	caryophyllene oxide	t	t	nt	t	t	nt
1627	1-epi-cubenol	t	t	nt	t	t	nt
1630	γ-eudesmol	t	t	nt	t	t	nt
1644	epi-α-muurolol	t	t	nt	t	t	nt
1649	β-eudesmol	t	t	nt	t	t	nt
1652	α-eudesmol	t	t	nt	t	t	nt
1652	α-cadinol	t	t	nt	t	t	nt
2312	abieta-7,13-diene-3-one	0.5	0.5	nt	t	t	nt

[a] KI = linear Kovats Index on DB-5 column

[b] Unidentified compounds less than 0.5% are not reported

[c] Based on FID response for individual compounds normalized by total FID response

[d] Based on the % of total oil data scaled by the total essential oil yields

[e] Compositional values less than 0.1% are denoted as traces (t)

[f] $*P \leq 0.05$, $**P \leq 0.01$, ns = not significant at $P = 0.05$. nt = not tested

stephensi has evolved highly efficient metabolic pathways to metabolize the PSCs present in juniper and often increases food intake and gains weight when consuming a juniper diet compared to when it is consuming the "non-toxic" control diet of rabbit chow (Haley et al. 2007; Skopec et al. 2007, 2013a, b; Skopec and Dearing 2011). Because of its physiological adaptations to consuming juniper, *N. stephensi* does not need to rely on behavioral mechanisms, such as caching, to minimize terpene intake (Torregrossa and Dearing 2009b; Torregrossa et al. 2011). However, obligate specialization does come at a cost; *N. stephensi* does not fare as well on novel diets as the generalist *N. albigula* and shows less dietary flexibility than the facultative specialist *N. lepida* (Skopec et al. 2015; Sorensen et al. 2005; Torregrossa et al. 2012).

Juniperus monosperma, the preferred food of *N. stephensi*, has a lower terpene content than *J. osteosperma* (Adams 1994; Adams et al. 2014a, b, 2016). *Juniperus monosperma* contains less than 0.6% dry weight terpenes while *J. osteosperma* ranges from 0.75–2.5% terpenes (this study, Adams et al. 2014a, 2016). Also, the terpene profile of *J. monosperma* is dominated by a single terpene, α-pinene, which comprises 50–60% of the terpene makeup (Adams et al. 2014a, b). The major terpenes in *J. osteosperma* are camphor, verbenol and bornyl acetate, which comprise 21–

Table 2 Significant oil components (% total oil basis and mg/g DM basis) for *J. osteosperma* from trees browsed and not-browsed by *N. albigula*

KI[a]	yields/ Compounds[b]	Browsed trees % oil[c]	Not-browsed % oil	*F* ratio	Browed trees mg/g DM[d]	Not-browsed mg/g DM	*F* ratio
932	**α-pinene**	**2.32**	**1.32**	**5.59***	**0.23**	**0.10**	**13.69 ****
1025	**β-phellandrene**	1.10	0.75	4.03 ns	**0.11**	**0.07**	**4.88 ***
1086	**terpinolene**	0.72	0.65	0.364 ns	**0.07**	**0.05**	**4.69 ***
1154	**sabina ketone**	**0.95**	**1.25**	**4.429 ***	0.10	0.10	0.00 ns
1204	**verbenone**	2.46	2.00	0.710 ns	**0.23**	**0.15**	**4.57 ***

[a] KI = linear Kovats Index on DB-5 column

[b] Unidentified compounds less than 0.5% are not reported

[c] Based on FID response for individual compounds normalized by total FID response

[d] Based on the % of total oil data scaled by the total essential oil yields $*P \leq 0.05$, $**P \leq 0.01$, ns = not significant at $P = 0.05$

Table 3 Protein perceptible phenolics (PPP), crude protein (CP) contents and correlations with essential oil (terpene) yields in leaves of *J. osteosperma* from trees browsed and not-browsed by *N. albigula*

Content	Source of juniper foliage		F ratio, significance
	Browsed	Not-browsed	
PPP (mg/g)	11.70 mg/g[b]	16.41 mg/g[b]	$F = 2.40$, $P = 0.14$ ns
CP (%)	6.148%[b]	6.146%[b]	$F = 7 \times 10^{-5}$, $P = 0.99$ ns
Correlations			
Terpene concentration (mg/g DM) vs. PPP (mg/g DM)	r = −0.067, t = 0.19, $P = 0.85$ ns[a]	r = −0.335, t = 0.871, $P = 0.41$ ns	
Terpene concentration (mg/g DM) vs. crude protein (%)	r = 0.150, t = 0.429, $P = 0.68$ ns	r = 0.228, t = 0.574, $P = 058$ ns	
PPP (mg/g DM) vs CP (%)	r = −0.019, t = 0.54, $P = 0.96$ ns	r = −0.725, t = 2.58, $P = 0.041$*	

[a] ns = not significant at $P = 0.05$ *$P \leq 0.05$

[b] Values with a common superscript are not significantly different at $P = 0.05$

23%, 11% and 8.5–12.5% respectively, of the terpenes present (Table 1). Because *J. monosperma* has a lower level of terpenes than *J. osteosperma*, and more than half of the terpene present in *J. monosperma* is α-pinene, highly efficient and specialized metabolic pathways for metabolizing α-pinene would allow for obligate specialization in *N. stephensi*.

Even though α-pinene is the dominant terpene present in *J. monosperma*, the much less abundant p-cymene (0.6–1% of total oils) is a possible feeding cue for *N. stephensi*, since browsed juniper trees were rich in p-cymene (Adams et al. 2014a). It is possible that *N. stephensi* has an upper threshold in its ability to distinguish concentrations of α-pinene and *J. monosperma* exceeds that threshold, so a less abundant terpene like p-cymene is used as a foraging cue. Both *N. lepida* and *N. albigula* chose to forage on *J. osteosperma* that had higher concentrations of α-pinene (4.5 vs 3.0% for *N. lepida* (Adams et al. 2016) and 2.3 vs 1.3% for *N. albigula* (Table 2)); however, α-pinene is much less abundant in *J. osteosperma* compared to *J. monosperma* (Adams et al. 2016). Further studies will be needed to look at thresholds of detection of both α-pinene and p-cymene in *N. stephensi* to see if these terpenes are used as feeding cues.

In an earlier study, little variation was detected in the terpene profiles of the browsed and not-browsed *J. monosperma* (Adams et al. 2014a). In some cases, herbivory causes increased production of terpenes to serve as cues to nearby plants, deterring further herbivory or attracting natural predators of invertebrate foragers (Theis and Lerdau 2003). In other

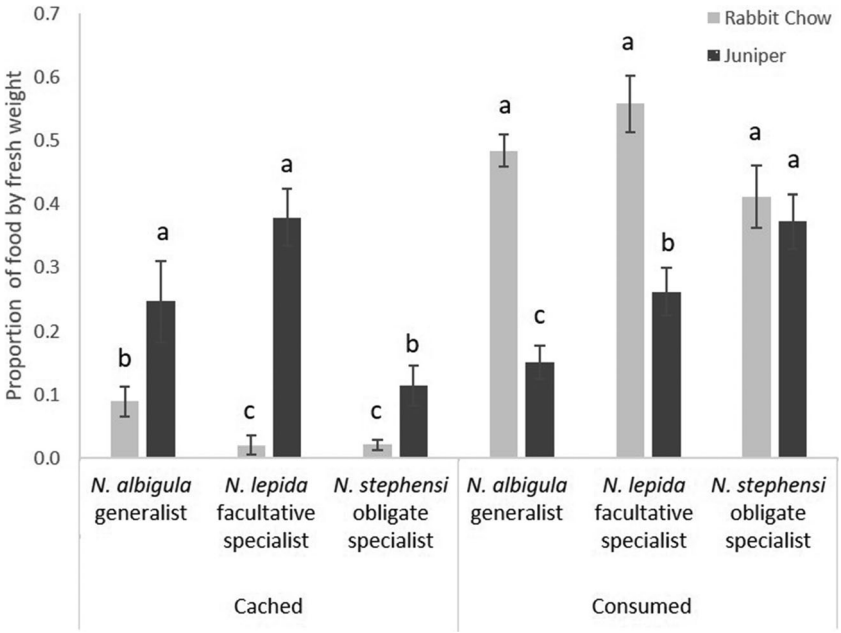

Fig. 1 Proportion of juniper versus rabbit chow cached or consumed by three species of woodrats. Means ± SE are shown. Letters a, b and c denote means that are significantly different ($P < 0.05$) within cached or consumed as determined by Tukey's HSD

Table 4 Comparison of results for three woodrat species that feed on juniper

Woodrat – juniper	Feeding behavior by woodrat	Browsed juniper selected for on a % total oil basis or mg/g dry matter basis:	Browsed juniper not selected for/ against:	Caches juniper in the lab	Proposed role of terpenes
N. stephensi – *J. monosperma*[a]	Obligate specialist, diet 90% juniper (Vaughan 1982)	**higher %** p-cymene	total oil yields PPP	No	Foraging and feeding cue
N. lepida – *J. osteosperma*[b]	Facultative specialist, diet 90% juniper (Skopec et al. 2015)	**higher %** α-pinene **lower %** α-campholenal **lower mg/g** p-cymene; α-campholenal sabina ketone terpinen-4-ol p-mentha-1,4-dien-7-ol	total oil yields PPP protein	Yes	Foraging and feeding deterrent
N. albigula – *J. osteosperma*	Generalist, diet 25% juniper (Dial 1988)	**higher % & mg/g** total oil yields **higher % & mg/g** α-pinene **higher mg/g** β-phellandrene terpinolene verbenone **lower %** sabina ketone	PPP protein	Yes	Foraging cue but feeding deterrent

PPP protein-precipitable phenolics

[a] Adams et al. 2014a

[b] Adams et al. 2016

cases, increased production of terpenes can attract mammalian herbivores as seen in the swamp wallaby that is attracted to damaged *Eucalyptus* (Finnerty et al. 2017). Further investigations into the relationship between *N. stephensi* and *J. monosperma* may shed light into the role of chemicals in establishing plant-mammaliam herbivore relationships. Specifically, if *N. stephensi* uses terpenes as feeding cues rather than feeding deterrents, successful individuals of *J. monosperma* may have a reduced response to herbivory, so as to not attract more woodrats. This could be tested by looking at terpene production by *J. monosperma* in response to mechanical damage, i.e. clipping, in areas with high *N. stephensi* abundance, and in areas with no woodrats.

Facultative specialists, such as *N. lepida*, have broader habitat niches than obligate specialists but can have limited available feed in certain parts of their range leading to dietary specialization (Shipley et al. 2009). *Neotoma lepida* has a large range size and specializes on a variety of plants depending on their availability. For example, *N. lepida* populations in the Great Basin Desert specialize on *J. osteosperma* (Skopec et al. 2015), while populations in the Mojave Desert specialize on creosote bush (*Larrea tridentata*, Cameron and Rainey 1972) or mesquite (*Prosopis glandulosa,* Smith et al. 2014), and populations from inland California specialize on Cholla cactus (*Opuntia bigelovii*, Brown et al. 1972) or prickly pear cactus (*Opuntia occidentalis*, MacMillen 1964). This adaptability towards a host plant may mean that *N. lepida* has a flexible but less efficient detoxification system for dealing with a wider variety of PSCs (Magnanou et al. 2009; Skopec et al. 2013a, b). Alternatively, these herbivores may rely on behavioral adaptations like detecting and avoiding plants high in PSCs, or may utilize caching as a means to allow VOCs to volatilize before consumption (Torregrossa and Dearing 2009a, b). We found that *N. lepida* chose to forage on juniper that was 1.5% higher in α-pinene but 3.3, 0.9, 0.3 and 0.2% lower in terpinen-4-ol, p-cymene, sabina ketone and p-mentah-1,4-dien-7-ol, and α-campholenal, respectively compared to not-browsed juniper (Adams et al. 2016). While foraged juniper was higher in one terpene compared to not-browsed juniper, the fact that they were lower in five different terpenes suggests that terpenes may act as feeding deterrents for *N. lepida*. In the behavioral trials, *N. lepida* cached more juniper than rabbit chow and cached more juniper than *N. stephensi. Neotoma lepida* also preferred to consume rabbit chow over juniper, further evidence that terpenes may act as feeding deterrents for *N. lepida* and that behavioral mechanisms are involved (i.e. caching) as part of *N. lepida's* response to terpenes. The use of behavioral mechanisms over specialized physiological mechanisms may allow greater flexibility in *N. lepida's* diet and therefore habitat (Skopec et al. 2015).

The dietary generalist *N. albigula* chose to browse on trees that are higher in terpenes overall: 1% higher in α-pinene, 0.35% higher in β-phellandrene, 0.07% higher in terpinolene, and 0.46% higher in verbenone and 0.3% lower in sabina ketone compared to not-browsed juniper (Table 2). As a generalist that can only consume a maximum of 30–50% juniper, due to a reduced ability to metabolize the PSCs present (Haley et al. 2007; Skopec et al. 2007; Sorensen et al. 2004b), we expected *N. albigula* to be highly deterred by terpenes and to choose to forage on plants lower in terpenes. However, *N. albigula* only seemed to avoid one compound, sabina ketone. It was already known that *N. albigula* utilizes caching as a mechanism to allow the terpenes present in juniper to volatilize, and juniper found in *N. albiqula* caches contains little to no detectable terpene (Torregrossa and Dearing 2009b). In the laboratory study, *N. albigula* cached more and ate less juniper than *N. stephensi,* showing that *N. albigula* is likely deterred from eating juniper with terpenes but not deterred from caching it. *Neotoma albigula* cached more rabbit chow than both *N. lepida* and *N. stephensi,* showing that it might have an overall greater propensity for food caching then the other two species.

All three species of woodrats cached a higher proportion of juniper compared to rabbit chow. Another generalist mammalian herbivore that relies heavily on food caching, the American pika (*Ochotona princeps*), preferentially caches plants higher in PSCs as a mechanisms of food preservation, since many PSCs are antimicrobial and antifungal and plants higher in PSCs had slower decomposition rates (Dearing 1997). A number of bird species bring plants high in VOCs to their nests to reduce parasite loads (Clark 1991; Petit et al. 2002; Wimberger 1984). Therefore, the woodrats preference for caching juniper could be an adaptive behavior to preserve cached foods or may be an adaptive behavior to decrease the number of parasites present in the middens.

It is possible that unmeasured VOCs influence the foraging and/or caching behavior of woodrats. Also, nutrient availability alters mammalian herbivore responses to VOCs, and mammals consuming higher nutrient diets tolerate higher doses of VOCs (Bedoya-Pérez et al. 2014). Alternatively, higher VOC contents found in trees browsed by *N. albigula* might act as an attractant, if greater terpene yields were correlated with higher amounts of nutrients such as protein. However, we saw no evidence that VOC levels were correlated with protein levels. While we did not see a difference in the crude protein and/or fiber levels of browsed versus not-browsed juniper in this or previous studies (Adams et al. 2014a, 2016), increasing the sample size of juniper trees analyzed may reveal a pattern between VOC levels and nutrient levels. While we have identified (Table 4) a number of VOCs that are potential feeding/foraging cues (p-cymene, α-pinene, β-phellandrene, terpinolene, verbenone) and deterrents (p-cymene, α-campholenal, sabina ketone, and terpinen-4-ol p-mentha-1,4-dien-7-ol), further studies are needed to determine each woodrat species' minimum and maximum thresholds for these VOCs.

The importance of taking a holistic view of the role of VOCs in foraging behavior of mammalian herbivores is highlighted by the differences in the juniper foraging and caching behavior that we observed in three species of woodrats that vary in their dependence on juniper as a food source. Our thorough understanding of the ecological relationship between each woodrat and juniper species, and the physiological responses of each woodrat species to the VOCs present in juniper, allowed us to interpret their behavioral responses to the VOCs present in juniper and place those into an ecological context. Further studies are needed to better understand how mammalian herbivores may be utilizing the VOCs produced by plants as either feeding or foraging deterrents or cues and the relationship between woodrats and juniper described herein may serve as an ideal study system.

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