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PLANT ANIMAL INTERACTIONS

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Plant secondary metabolites alter the feeding patterns of a mammalian herbivore (*Neotoma lepida*)

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Abstract Mammalian herbivores are predicted to regulate concentrations of ingested plant secondary metabolites (PSMs) in the blood by modifying the size and frequency of feeding bouts. It is theorized that meal size is limited by a maximum tolerable concentration of PSMs in the blood, such that meal size is predicted to decrease as PSM concentration increases. We investigated the relationship between PSM concentration in the diet and feeding patterns in the herbivorous desert woodrat (*Neotoma lepida*) fed diets containing phenolic resin extracted from creosote bush (*Larrea tridentata*). Total daily intake, meal size and feeding frequency were quantified by observing the foraging behavior of woodrats on diets containing increasing concentrations of creosote resin. Desert woodrats reduced meal size as resin concentration in the diet increased, resulting in an overall reduction in daily intake and regulation of resin intake. Moreover, desert woodrats were able to detect resin concentrations in the diet and regulate the intake of resin very rapidly. We suggest that the immediate and sustained ability to detect and regulate the intake of resin concentrations during each foraging bout provides a behavioral mechanism to regulate blood concentrations of resin and allows desert woodrats to make "wise" foraging decisions.

Keywords Creosote bush · Desert woodrat · Feeding frequency · Meal size · Phenolic resin

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Introduction

Ingestion of plant secondary metabolites (PSMs) presents a major challenge to mammalian herbivores. PSMs that are ingested and absorbed enter the general circulation where they can be distributed to various tissues and organs. The accumulation of PSMs in tissues and organs can have severe physiological consequences such as lesions, cysts, metabolic acidosis and death (Grice et al. 1968; Jha and Chugh 2003; Koppel et al. 1981; Lambert et al. 2002; Majak 1992; Robles et al. 1998). The severity of the physiological consequences induced by PSMs is dependent on the concentration of PSMs that accumulate in the tissues (Paumgartten et al. 1990; Sperling et al. 1967). Mammalian herbivores are expected to employ physiological and behavioral strategies that maintain concentrations of PSMs in the blood below critical levels that cause physiological damage.

Theory predicts that herbivores regulate the concentration of PSMs in the blood below critical levels by modifying foraging patterns (Brattsten 1979; Foley et al. 1999). Specifically, preliminary models suggest that mammalian herbivores reduce meal size as concentration of PSMs in the diet increase, thereby maintaining a constant blood concentration of PSMs below some critical threshold. The models further suggest that feeding frequency is a function of detoxification and elimination, i.e., feeding frequency increases with detoxification rate. These models assume that mammalian herbivores have the ability to determine the concentration of PSMs in the diet, as well as the body and, can appropriately modify foraging behavior on a fine scale (i.e., within a 24-h period). To date, only a single study has empirically demonstrated that patterns of intake are influenced by PSM concentration in the diet. Wiggins et al. (2003) found that brushtail possums (*Trichosurus vulpecula*) detected increasing concentrations of a PSM over a 24-h period and regulated the intake of PSMs within that feeding period by altering the size and frequency of feeding bouts. The relationship

between PSM concentrations in the diet and fine scale foraging patterns is important in understanding the link between physiological and behavioral mechanisms that serve to mitigate the consequences of ingested PSMs and maximize daily food intake.

The aim of this investigation was to identify the relationship between PSM concentrations in the diet and daily feeding patterns using the desert woodrat (*Neotoma lepida*) fed PSMs from their natural diet, creosote bush (*Larrea tridentata*). Populations of desert woodrats in the Mojave are considered specialized foragers in that they naturally consume significant quantities of creosote bush (Cameron and Rainey 1972; Karasov 1989; Meyer and Karasov 1989). Creosote bush contains large concentrations of phenolic resin (11–26% by dw), of which nordihydroguaiaretic acid (NDGA) can comprise up to 40% (Rhoades and Cates 1976; Mabry et al. 1977). NDGA is a known feeding deterrent for a variety of herbivores, including desert woodrats (Mangione et al. 2000; Meyer and Karasov 1989; Rhoades 1977a, b; Rhoades and Cates 1976). However, desert woodrats naturally consume up to twice the dose of NDGA each day (3.3–7.8% by dw) that causes cysts and kidney disease in laboratory rats (0.5–3% by dw; Grice et al. 1968). Desert woodrats may therefore possess a variety of physiological and behavioral mechanisms that mitigate the toxic consequences of creosote resin. This study investigated one behavioral mechanism, altered foraging patterns, that may allow desert woodrats to regulate concentrations of creosote resin, and therefore NDGA, below critical (i.e., toxic) levels in the body.

We hypothesized that desert woodrats would regulate the intake of creosote resin and maximize food intake as concentrations of PSMs in the diet increased through reduced meal size coupled with increased feeding frequency. The affect of PSM concentration on meal size and frequency was determined by examining the feeding patterns of desert woodrats every 60 s across various concentrations of creosote resin in the diet.

Materials and methods

Animals

Neotoma lepida were collected from the Mojave Desert near Beaver Dam, Utah (37° 06′N, 113° 58′W) during 7–9 May 2001. Desert woodrats were transferred to the University of Utah Animal Facility and maintained in shoebox cages (48×27×20 cm^3) on a 12–12 light-dark cycle at 28–29°C. Desert woodrats were provided water and Harland Teklad rabbit chow (formula 2031) ad libitum prior to experimentation.

Resin extraction and diet preparation

Desert woodrats were fed diets containing various concentrations of resin extracted from creosote bush. Creosote resin was extracted from leaves collected in the field. Creosote leaves were collected randomly from eight to ten *Larrea tridentata* bushes at the same site and time as desert woodrats were collected. A collection of both young and mature leaves was stripped from branches by hand. Leaves were placed immediately on dry ice until arrival at the University of Utah, where they were stored at −20°C. Resin was extracted from creosote foliage by submerging creosote leaves in ethyl ether for 45 min (1:6, wet leaf mass:volume solvent). The extract was filtered (Whatman no. 10 paper) and ethyl ether was evaporated from the resin extract using a rotovap until the resin was a dense, viscous consistency. The remaining ethyl ether was removed from the resin using a vacuum pump for 48 h. The extraction procedure yielded a powdered resin that was 4.7% of the dry weight of the leaves. The resin was stored at −20°C for less than 5 months prior to use.

Resin diets were prepared by dissolving the desired amount of resin into ethyl acetate and applying the ethyl acetate–resin mixture to ground rabbit chow (Harland Teklad, formula 2031) using a volume equal to 25% of the dry weight of chow. The resin treatments included 0, 1.5, 3 and 6% resin per unit dry weight of chow. This range of concentrations includes the upper (6%) and lower (1.5%) dietary concentrations of resin naturally consumed by desert woodrats (Cameron and Rainey 1972; Karasov 1989; Meyer and Karasov 1989). The 0% diet was prepared by applying ethyl acetate to the chow (25% by dw). Ethyl acetate was completely evaporated from all resin treatments in a fume hood as confirmed gravimetrically. Diet treatments were stored at −20°C until use.

Feeding experiment

The foraging patterns of eight desert woodrats were evaluated by examining feeding activity on each of the four diet treatments. Woodrats were given one of each of the four treatments once every 8 days in a random order to avoid affects of acclimation to resin treatments. Woodrats were fasted for 24 h prior to each resin treatment to ensure that animals were motivated to feed. Preliminary studies indicated that desert woodrats would not consume diets containing 6% resin unless they had been food restricted prior to offering the diet. Body mass was recorded immediately prior to the offering of each resin treatment. Woodrats were offered each resin treatment in excess of mass requirements (~15 g) and given water ad libitum at 1600–1700 hours. Each resin treatment was offered for 16 h. Woodrats had continuous access to the diet treatment that was located in a feeding chamber (Nalgene 650-0104) on the side of their cage. Woodrats were acclimated to the feeding chamber for at least 3 days prior to experimentation during which time they were fed untreated, powdered rabbit chow (Harland Teklad 2031). They were also fed rabbit chow for the 7 days between each resin treatment.

Feeding patterns were measured for desert woodrats on each of the four resin treatments. Specifically, total

food intake, average meal size, size of first meal, number of meals, feeding interval and feeding rate were measured using a feeding chamber placed on an Ohaus Navigator scale (sensitivity = 0.1 g). Date, time and mass of resin treatment were relayed from the balance every 60 s and recorded by a Toshiba T4500 computer. All resin treatments were 98% dry and water content did not change during the 16 h feeding period. Therefore, dry mass of resin treatments at any give time period was calculated as:

Recorded mass × 0.98

Computerized measurements of the mass of diet remaining and a time stamp provided accurate measurements of the start time of a feeding bout, duration of a bout, and amount eaten. The start of a "meal" was defined as any change in mass > 0.1 g that occurred within a period of 2 min or less. The end of a meal was defined as the initial time when constant mass lasted a minimum of 4 min. Video observations of a sub-sample of desert woodrats on both 0 and 6% resin treatments indicated that 4 min was the minimum amount of time necessary for animals to exit the feeding chamber and engage in other activities (e.g., grooming, drinking, resting, etc.). Total food intake was calculated as the dry matter intake (DMI) during the entire 16 h feeding period. Meal size was calculated as the net decrease in mass from the start of the meal to the end. Meal intervals were calculated as the time between meals. Feeding rate was calculated as mass (DMI) consumed per minute during periods of feeding (i.e., periods of time when the mass of diet changed).

Prediction of unregulated resin intake

To determine whether desert woodrats were regulating resin intake, a comparison was made for each of the treatment diets between actual resin intake and a predicted resin intake if animals did not alter food intake. Actual resin intake, both total and per meal, was calculated as:

Intake (DMI)
× resin proportion (either 0, 0.015, 0.03, or 0.06)

for each treatment. The unregulated resin intake on each treatment was estimated by predicting the resin intake as if food intake on the 0% resin treatment was maintained across all resin treatments. For example, if an animal consumed 8.2 DMI on the 0% resin treatment, then the hypothetical resin intake on a 1.5% resin treatment was calculated as:

8.2 DMI × 0.015.

Statistical analyses

All statistical analyses were performed using JMP software for Macintosh (JMP 2000). Intake was calculated on a per gram body mass basis due to variation in body mass among individual desert woodrats. Dry matter intake (DMI $\text{day}^{-1}\ \text{kg}^{-1}$), average meal size (DMI $\text{meal}^{-1}\ \text{kg}^{-1}$), size of first meal (DMI kg^{-1}), number of meals, feeding interval (min) and feeding rate (DMI min^{-1}) were analyzed using separate repeated measures ANOVAs with resin treatment (0, 1.5, 3 or 6%) as the within subjects effect. Comparisons between each resin treatment were analyzed using a Tukey's LSD. Analyses performed on resin intake only concerned diets containing resin and were therefore restricted to comparisons between 1.5, 3 and 6% resin treatments. The effect of period (i.e., time) was compared for each feeding parameter using separate repeated measures ANOVAs with time (first, second, third and fourth treatment) as the within subjects effect.

Results

Body mass (g) did not differ among resin treatments ($F_{(3,5)} = 2.52$, $P = 0.17$; 0% = 136.5 ± 8.48, 1.5% = 146.9 ± 7.92, 3% = 140.8 ± 8.63, 6% = 137.6 ± 7.68). In addition, body mass was not correlated with any of the feeding parameters for any of the resin treatments. There was no period effect for dry matter intake (DMI $\text{day}^{-1}\ \text{kg}^{-1}$; $F_{(3,5)} = 1.24$, $P = 0.39$), daily resin intake (g resin $\text{d}^{-1}\ \text{kg}^{-1}$; $F_{(3,5)} = 0.84$, $P = 0.53$), average meal size (DMI $\text{meal}^{-1}\ \text{kg}^{-1}$; $F_{(3,5)} = 1.67$, $P = 0.29$), resin intake per meal (g resin $\text{meal}^{-1}\ \text{kg}^{-1}$; $F_{(3,5)} = 0.39$, $P = 0.77$), size of first meal (DMI kg^{-1}; $F_{(3,5)} = 0.68$, $P = 0.60$), number of meals ($F_{(3,5)} = 1.16$, $P = 0.41$), feeding interval (min; $F_{(3,5)} = 1.79$, $P = 0.29$) and feeding rate (DMI min^{-1}; $F_{(3,5)} = 1.73$, $P = 0.28$).

Resin concentration did not influence the number of meals consumed each night or the intervals between meals. Woodrats consumed between 14.6 and 16 meals each night regardless of resin concentration in the diet ($F_{(3,5)} = 0.11$, $P = 0.95$). The interval between meals ranged from 54 and 62 min regardless of resin concentration ($F_{(3,5)} = 0.23$, $P = 0.87$).

Resin concentration did influence total intake in desert woodrats. Desert woodrats decreased total intake (DMI $\text{day}^{-1}\ \text{kg}^{-1}$) as resin concentration in the diet increased ($F_{(3,5)} = 6.90$, $P = 0.03$; Fig. 1). Desert woodrats consumed less than half as much on a 6% resin treatment than on the 0% treatment. The 1.5% and 3% resin treatments did not differ significantly from the 0% treatment. Although total intake decreased, the amount of resin consumed daily (g resin $\text{day}^{-1}\ \text{kg}^{-1}$) increased as the concentration of resin in the diet increased ($F_{(2,6)} = 7.24$, $P = 0.03$; Fig. 1). Desert woodrats consumed less than half as much resin on the 1.5% resin treatment as they did on the 6% treatment, whereas the 3% diet did not differ from any other treatment. However, actual resin intake on each resin treatment was lower than the predicted unregulated resin intake (Fig. 1). For example, if desert woodrats had maintained

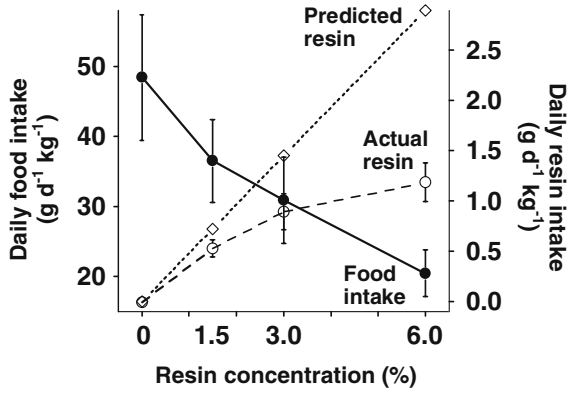

Fig 1 Total daily food intake (g dry matter intake per kg body mass [*filled circle*]) from a diet containing increasing concentrations of phenolic resin (0, 1.5, 3 and 6% by dry weight) and subsequent actual resin intake (*open circle*) compared to predicted unregulated resin intake (*open diamond*) in desert woodrats. Actual resin intake was calculated based on total daily intake and the concentration of resin in each diet treatment. Unregulated resin intake was estimated as the amount of resin that would have been consumed in each resin treatment if desert woodrats had maintained total daily intake equivalent to the 0% resin treatment (48.4 ± 8.95 g day^{-1} kg)

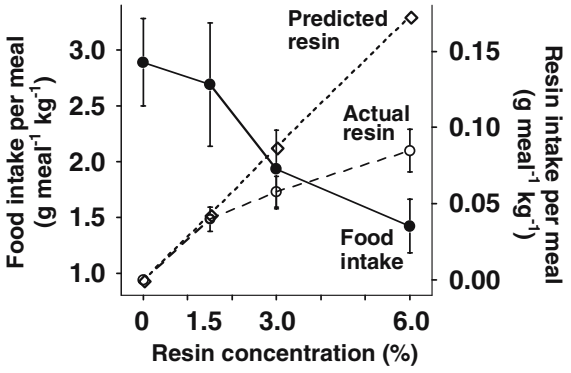

Fig 2 Total food intake per meal (g dry matter intake per meal per kg body mass [*filled circle*]) from a diet containing increasing concentrations of phenolic resin (0, 1.5, 3 and 6% by dry weight)) and subsequent actual resin intake per meal (*open circle*) and predicted unregulated resin intake per meal (*open diamond*) in desert woodrats. Actual resin intake consumed per meal was calculated based on intake per meal and the concentration of resin in each diet treatment. Unregulated resin intake was estimated as the daily amount of resin that would have been consumed per meal in each resin treatment if desert woodrats had maintained meal size equivalent to the 0% resin treatment (2.89 ± 0.39 g meal^{-1} kg)

food intake consistent with the 0% resin treatment (48.37 ± 8.95 DMI day^{-1} kg^{-1}) while consuming a diet of 6% resin, the unregulated total resin intake (2.90 g resin day^{-1} kg^{-1}) would have been 2.4×greater than the actual total resin intake (1.23 ± 0.20 g resin day^{-1} kg^{-1}).

Resin concentration also influenced the size of meal consumed by desert woodrats. Meal size (DMI meal^{-1} kg^{-1}) decreased as resin concentration in the diet increased ($F_{(3,5)} = 15.77$, $P = 0.006$; Fig. 2). The meal size on the 6% resin treatment was nearly half that of the 0% and 1.5% treatments. Despite a decrease in meal size, desert woodrats increased the quantity of resin consumed per meal as resin concentration in the diet increased ($F_{(2,6)} = 7.20$, $P = 0.03$; Fig. 2). Desert woodrats consumed over twice the quantity of resin per meal on a 6% resin treatment compared to the 1.5% treatment, whereas 3% did not differ from any other treatment. However, actual resin consumed per meal as resin concentrations in the diet increased was lower than predicted if resin intake was not regulated (Fig. 2). For example, if desert woodrats had maintained the same meal size as on the 0% resin treatment (2.89 ± 0.39 DMI meal^{-1} kg^{-1}) while consuming a 6% resin treatment, the predicted unregulated resin intake per meal (0.17 g resin meal^{-1} kg^{-1}) would have been twice that of the actual resin consumed per meal (0.09 ± 0.014 g resin meal^{-1} kg^{-1}).

In addition, the size of first meal consumed each night tended to decline as resin concentration in the diet increased ($F_{(3,5)} = 3.90$, $P = 0.09$, Fig. 3). Although the repeated measure analysis was only marginally significant, the average size of the first meal on the 0% treatment (4.48 ± 1.25 DMI meal^{-1} kg^{-1}) was 3.5×greater than that on the 6% resin treatment (1.27 ± 0.29 DMI meal^{-1} kg^{-1}; Tukeys LSD; $P < 0.05$).

Resin concentration also influenced the rate at which food was consumed. Desert woodrats consumed food at a slower rate on the 6% resin treatment (0.12 ± 0.006 DMI min^{-1}) than on all other treatment diets (0% = 0.16 ± 0.01, 1.5% = 0.16 ± 0.01, 3% = 0.15 ± 0.006; $F_{(3,5)} = 9.53$, $P = 0.02$, Fig. 4).

Discussion

We tested the hypothesis that mammalian herbivores regulate the concentration of PSMs consumed by modifying foraging patterns. We found that desert woodrats were capable of regulating the quantity of PSMs in-

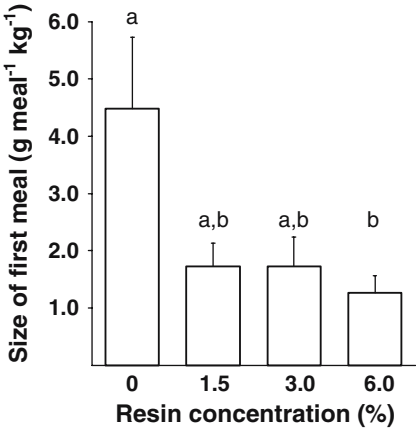

Fig 3 Average size of the first meal (g dry matter intake per meal per kg body mass; + SE) consumed by desert woodrats as resin concentration in the diet increased. *Different letters* represent significant differences between resin treatments (Tukeys LSD; $P < 0.05$)

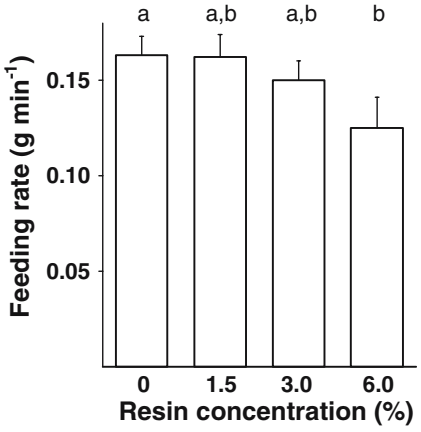

Fig 4 Average feeding rate (g dry matter intake per min; + SE) by desert woodrats fed diets containing increasing concentration of resin. *Different letters* represent significant differences between resin treatments (Tukeys LSD; $P < 0.05$)

gested from creosote bush by reducing meal size as resin concentration in the diet increased. However, desert woodrats did not compensate for a reduction in meal size by increasing the number of meals (i.e., frequency) and therefore total intake was reduced as resin concentration in the diet increased. Moreover, the reduction in feeding rate caused by the increasing resin concentrations, suggests that creosote resin limits herbivory by not only reducing intake, but also by compromising the feeding rate of desert woodrats. In the subsequent paragraphs, we discuss the capacity and limitations of desert woodrats in regulating the intake of creosote resin and place these results in an ecological framework.

This study demonstrated that the intake of PSMs from creosote bush can be regulated at several temporal scales. Previous studies focused on how mammalian herbivores regulate PSM intake on a daily basis (Pfister et al. 1990, 1997; Stapley et al. 2000). However, theoretical work (Foley et al. 1999) and a single empirical study (Wiggins et al. 2003) suggest that the ability to detect and regulate PSM intake occurs at a much finer temporal scale. Our data support these studies in showing that desert woodrats instantaneously (within a minute) regulate the intake of PSMs in creosote resin by reducing meal size as resin concentration increases.

The reduction in meal size with increasing dietary resin concentration indicates that creosote intake in desert woodrats may be driven by the upper resin threshold (presumably as detected via blood concentrations) that can be tolerated. In keeping with this hypothesis, reduction in meal sizes across resin treatments resulted in resin intake levels that were half the predicted intake levels if meal size was not regulated (Figs. 1, 2). Moreover, the observed reduction in meal size may assist, along with detoxification mechanisms, in minimizing lethal levels of NDGA, a dominant and toxic PSM in creosote resin (Dearing et al. 2002; Grice et al. 1968; Mabry and Gill 1979; Mangione et al. 2001). The estimated quantity of NDGA consumed per meal on the 6% resin treatment (~36 mg meal^{-1} kg^{-1}) was half the LD_{50} dose (75 mg meal^{-1} kg^{-1}, concentration at which mortality occurs in 50% of animals) of NDGA in mice (Lambert et al. 2002). If woodrats did not decrease food intake as resin concentrations increased on the 6% treatment, the dose of NDGA ingested (~68 mg meal^{-1} kg^{-1}) would have been nearly equal to the LD_{50} dose for mice.

There may be some concern that desert woodrats did not regulate resin intake adequately since resin intake increased as resin concentration in the diet increased and did not reach a true plateau. However, given that intake on 3 and 6% resin treatments did not differ, our results suggest that desert woodrats had reached their threshold for resin intake. Although the maximum daily intake of resin in our study (172 mg resin day^{-1}) was much lower than resin intake by desert woodrats in a previous study when a plateau was reached (310 mg resin day^{-1}; Mangione et al. 2000), differences are likely due to the time of acclimation with resin diets. Desert woodrats in the Mangione et al. (2000) study were fed resin treated diets for six days compared to a single day in our study. Finally, we argue that increased resin intake, despite decreases in meal size as resin concentration increased, emphasizes the conflict between minimizing resin intake and maximizing energy intake. It is likely that energy demands result in greater intakes than predicted at higher resin concentrations.

An ability to regulate resin intake by desert woodrats is consistent with previous work conducted on a different mammalian herbivore fed PSMs from a different chemical class. Wiggins et al. (2003) fed brushtail possums (*Trichosurus vulpecula*) diets of increasing concentrations of cineole (0, 6.8 and 15.3% by dry weight), a PSM present in *Eucalyptus* leaves. In their study, brushtail possums decreased total daily intake, meal size and feeding rate as cineole concentration in the diet increased. Desert woodrats and brushtail possums are phylogenetically and geographically distinct and consume plant species that differ quantitatively and qualitatively in their chemical defenses. The creosote resin fed to desert woodrats is comprised of phenolics, which are in an entirely different chemical class than the terpene, cineole, fed to brushtail possums. Despite differences in phylogeny, diet and PSMs used in these studies, both desert woodrats and brushtail possums altered foraging patterns in a consistent manner when PSM concentrations in the diet increased. Taken together, these results suggest that the ability to detect varying concentrations of PSMs and subsequent modification of meal sizes may be a common strategy employed by mammalian herbivores to minimize PSMs in the body.

Our study suggests that desert woodrats are capable of rapidly assessing PSM concentrations and modifying feeding behavior accordingly. The reduction in the size of the first meal as resin concentration increased indicates animals immediately respond to differences in PSM concentrations. This ability to promptly respond is consistent with information on the rate at which PSM

concentrations can increase in the blood following a single dose of ingested PSMs. For example, PSMs such as alpha-pinene can reach blood concentrations that are potentially lethal to mammals within minutes following oral ingestion (Sorensen and Dearing 2003). Although the pharmacokinetics of creosote resin in the blood has not been investigated, the response to increasing concentrations of resin by desert woodrats suggests a tight link between increases in blood concentrations of resin and feeding response. Such a connection would allow mammalian herbivores to rapidly assess the concentrations of PSMs in individual plants thereby permitting the selection and consumption of plants with low PSM concentrations.

There are several mechanisms that may explain the ability of desert woodrats to rapidly detect and respond to increasing concentrations of resin in the diet. Reactions that occur directly in the mouth prior to absorption can have immediate effects on intake. For example, the bitter taste of some PSMs are thought to explain intake reduction in mammalian herbivores (Bate-Smith 1972; Bernays 1990; Edwards 1978; Foley et al. 1999). The buccal cavity is also enriched with trigeminal nerves that are stimulated by both the taste and smell of PSMs (Silver 1987) and can elicit an immediate cessation of feeding (Jakubas and Mason 1991). In addition, intake levels can be associated with postingestive consequences of absorbed PSMs, such as emesis, and herbivores will often avoid plants that trigger this association (Pfister et al. 1990; Provenza 1995, 1996, 1994, 1998). Avoidance of PSMs due to postingestive consequences may be particularly effective in mammalian herbivores that have had previous ecological experience with PSMs. That desert woodrats naturally consume creosote and therefore have experience with the negative physiological consequences of creosote resin (Cameron and Rainey 1972; Dearing et al. 2002; Karasov 1989; Mangione et al. 2000, 2001; Meyer and Karasov 1989) suggests that desert woodrats may use a combination of nasal and oral cues and previous experience to rapidly assess the quantity of resin in the diet that can be tolerated.

Although desert woodrats were able to detect and regulate the intake of creosote resin, they were not able to alter feeding patterns in such a way to maintain intake. An inability of desert woodrats to increase feeding frequency as resin concentration increased is likely due to limitations of the rate of detoxification. Theory predicts that feeding frequency is dependent on the rate at which PSMs are detoxified and eliminated from the body, such that an animal will not consume a subsequent meal until the PSM that enters the blood from the first meal is adequately eliminated though detoxification mechanisms (Foley et al. 1999). Although desert woodrats reduced meal size, the total and per meal dose of resin ingested increased. It is not expected that animals could feed more frequently as resin intake increased unless they increased the rate at which resin is detoxified and eliminated from the body. Limitations on the rate of detoxification and elimination may partially explain why desert woodrats reduced feeding rates as resin concentration in the diet increased. However, detoxification enzymes typically require three days of exposure to PSMs before they are fully induced and functioning at maximum capacity (Sipes and Gandolfi 1986). Because desert woodrats in the present study were not acclimated to creosote resin, their detoxification enzymes may be operating at a much lower capacity than wild animals whose enzymes are constantly induced due to chronic ingestion of PSMs. We predict that desert woodrats under a natural state of enzyme induction (i.e., acclimated to creosote resin) could increase feeding frequency as resin concentration in the diet increases and would therefore be able to maximize total intake even as meal size decreases.

These data provide further support for the hypothesis that mammalian herbivores are capable of detecting PSM concentrations in the diet and can subsequently regulate intake. It is proposed that the ability to regulate PSM intake is directly related to mechanisms that detect blood concentrations of PSMs and the physiological need to keep blood concentrations below critical levels (Foley et al. 1999; Wiggins et al. 2003). The tight link between physiological processes, such as rates of detoxification, and behavioral modifications, such as temporal changes in foraging, emphasizes that PSMs are an important parameter in developing foraging theories. Additional experiments that vary both resin concentration in the diet and rate of release of resin in the body are needed to isolate the specific effects of toxicity threshold and detoxification capacity on foraging patterns of desert woodrats.

Ecological and evolutionary implications

Our laboratory study supplements that of other studies on desert woodrats foraging under natural field conditions. Thompson (1982) observed that radio-collared woodrats visit a subset of available creosote bushes and tend to select, and therefore avoid, the same bushes each night. Although the resin chemistry of the selected bushes was not examined in Thompson's study, resin concentration is known to vary from 11–26% (by dw) within and between bushes (Rhoades and Cates 1976). Given, the home range size of an individual desert woodrat (550 m) and the density of creosote bushes (~1 every 3 m, Thompson 1982), there is likely to be high variation in resin concentration in the bushes a desert woodrat encounters each night. In addition, woodrats spent very little time foraging at each bush (Thompson 1982), suggesting that decisions regarding resin concentration and the quantity consumed must be made quickly. Furthermore, Karasov (1989) documented that woodrats in the field can identify and prefer plants and leaves with lower resin concentrations. Our study complements these existing field studies by demonstrating that woodrats have the ability to rapidly distinguish among differing resin concentrations comparable to re-

sin variation in nature. Our results also indicate that woodrats can respond rapidly to differing resin concentrations by adjusting meal size.

Given the field (Karasov 1989) and laboratory (this study) evidence that desert woodrats can identify and select plants with lower concentration, there may be strong selection for creosote bush to produce large quantities of resin. If desert woodrats cannot find a suitable resin concentration, they must reduce intake due to a reduction in feeding rate or consume alternative plants. These constraints may select for desert woodrats that can tolerate higher concentrations of creosote resin, through a combination of modified feeding behavior and enhanced detoxification mechanisms. These characteristics may explain how desert woodrats have successfully inhabited areas dominated by plants containing large quantities of PSMs that are unpalatable to most herbivores.

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