

Evolutionary irony: evidence that ‘defensive’ plant spines act as a proximate cue to attract a mammalian herbivore

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Many plants produce structural defenses to deter feeding by herbivores. However, many previous studies testing whether spines are effective at defending against mammalian herbivores have produced equivocal results. These ambiguous results are hypothesized to be due to herbivore counter-adaptations. We investigated potential counter-adaptations in a population of white-throated woodrats *Neotoma albigula* that specialize on cactus by investigating feeding behavior and preference for cacti varying in spinescence. *Neotoma albigula* exhibited a unique behavior of clipping cactus spines, which renders these defenses ineffective. Strikingly, these woodrats chose to collect spiny cacti over experimentally de-spined cacti, demonstrating that spines act as a proximal cue that attracts woodrats. This attraction is likely due to the higher protein and lower fiber content of spiny cacti compared to naturally non-spiny cacti. Thus, the ‘defensive’ spines of cacti are ineffective against a specialist herbivore and instead serve as an indicator of nutritional quality that promotes herbivory. Our results support the ‘rule-of-thumb’ hypothesis of foraging, which states that herbivores forage according to obvious visual cues that are indicative of nutritional content, rather than sampling nutrient composition of plants. We propose that specialist herbivores are unique systems in which to study other counter-adaptations to structural defenses and ‘rule-of-thumb’ foraging strategies.

The evolutionary arms race between plants and herbivores has generated numerous adaptations and counter-adaptations in both players. For instance, many plants defend themselves with toxic chemical compounds (Rhoades 1979). In response, herbivores have evolved appropriate detoxification strategies (Freeland and Janzen 1974, Dearing et al. 2005a). Many plants also utilize structural defenses, such as spines, hairs or thickened leaves (Hanley et al. 2007). Much less is known about the effectiveness and counter-adaptations of herbivores to structural defenses compared to chemical defenses (Hanley et al. 2007).

For instance, it is still questioned whether one type of structural defense, spinescence, is effective at deterring mammalian herbivores (Hanley et al. 2007). Spines and thorns are effective at limiting herbivory by some large (Cooper and Owen-Smith 1986, Wilson and Kerley 2003b) and small-bodied mammalian herbivores (Cooper and Ginnett 1998). However, other studies show no effect of spines on rates of herbivory (Cooper et al. 2003), nor any differences among herbivore species (Woodward and Coppock 1995). Disparate results have also been found between captivity- and field-based experiments (Potter and Kimmerer 1988, Cash and Fulbright 2005). It has been proposed that herbivore counter-adaptation to spinescent plants drives these equivocal results (Cooper et al. 2003, Hanley et al. 2007). While examples of counter-adaptations to plant physical defenses are common in invertebrates (Cardoso 2008, Keathley

and Potter 2011), there are few cases of them in vertebrate herbivores.

We investigated the effectiveness of cactus spines as a defense using woodrats *Neotoma* spp., small, herbivorous rodents common in the southwestern USA. Spines of blackbrush *Acacia rigidula* are effective at limiting herbivory in one species, the southern plains woodrat (*Neotoma micropus* (Cooper and Ginnett 1998). However, *N. micropus* is a dietary generalist and does not consume large amounts of this plant (Braun and Mares 1989). Our study focused on another species, the white-throated woodrat *N. albigula*. This species is a generalist herbivore, with some populations that facultatively specialize on *Opuntia* cactus (Vorhies and Taylor 1940, Macedo and Mares 1988). Specialist populations are adept at feeding and transporting heavily defended cacti and even remove spines from cacti to make them easier to handle (Richardson 1943). These behavioral adaptations allow *N. albigula* to cause substantial damage to cacti and lower their reproductive output (Hayes et al. 2013).

Woodrats are also interesting study animals given that they tend not to consume plants in situ, but collect them for subsequent consumption. Thus, their herbivory has two components: collection and feeding. First, woodrats forage to collect plant material and return it to their nest, or midden (Torregrossa and Dearing 2009). Because plant tissue is being removed at this step, it represents herbivory from the plants’ perspective. Collected plant material is often

stored for a period of time, during which it is consumed by the woodrats (Torregrossa and Dearing 2009). Structural defenses may impact both collection and feeding abilities of woodrats.

We conducted a number of experiments to understand interactions between specialist woodrats and the structural defenses of cacti. First, we characterized the diet of *N. albigula* at Castle Valley, to ensure that this population specialized on cacti. Next, we documented the variability of structural defenses among cacti. Plant investment in structural defenses can vary widely within a species. For example, individual cacti of *Opuntia lindheimeri* can range from those lacking spines to those completely covered in spines (Chavez-Ramirez et al. 1997). Understanding the variation in our system is important since woodrats forage in the context of this variation. Next, we tested the efficacy of cactus spines at defending plants against herbivory by *N. albigula* in a variety of feeding and choice trials. We predicted that this specialist would not be impeded by structural defenses. This result would offer an example of herbivore counter-adaptation to structural defenses, and help to clarify the ambiguous results of many previous studies testing whether plant spinescence is an effective defense. Last, we measured the nutrient composition of cacti exhibiting differing structural defenses to understand how nutrients might be influencing foraging choices.

Methods

Characterization of feeding in nature

The population of white-throated woodrats *Neotoma albigula* used in this study came from Castle Valley, UT (38°38'N, 109°18'W). While some populations of *N. albigula* are known to facultatively specialize on cacti (Vorhies and Taylor 1940, Macedo and Mares 1988), the feeding behavior of woodrats at Castle Valley has not been documented. Therefore, we first determined the natural diet of this population using stable isotope analysis to ensure that this population specializes on cactus. *Neotoma albigula* were caught in December 2011 (n = 2), March 2012 (n = 3), and November 2012 (n = 5), using Sherman live-traps baited with peanut butter and oats. All woodrats were transported to the Dept of Biology Animal Facility at Univ. of Utah and housed in individual cages (48 × 27 × 20 cm) under a 12:12-h light:dark cycle, with 28°C ambient temperature and 20% humidity in accordance with the Univ. of Utah Animal Care and Use Committee protocols 10-01013 and 12-12010.

Feeding in nature was characterized using stable isotope analysis. Hair samples were collected from the hindquarters of the animals at capture. We also collected samples of the dominant plants: juniper *Juniperus osteosperma*, sagebrush *Artemisia* spp. and cactus *Opuntia macrorhiza* × *O. polyacantha* hybrids (n = 3 individuals per species). All samples were brought to the Univ. of Utah for stable isotope analysis. Plant samples were dried and ground in a mill to pass through a 1 mm mesh screen. We analyzed the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of hair and plant samples using an elemental analyzer coupled with an isotope ratio mass

spectrometer and previously established methods (Baugh et al. 2004). We generated a prediction for the isotopic signature of woodrat hair assuming they were consuming a diet of 100% cactus by using the diet-tissue fractionation rates measured in rabbits of 3.4‰ for $\delta^{13}\text{C}$ and 2.8‰ for $\delta^{15}\text{N}$ (Sponheimer et al. 2003a, b).

Variability of structural defenses in nature

Many plants exhibit variation in physical defenses in nature, allowing herbivores to select plants of differing defenses. We inventoried the cacti at Castle Valley to document the variability in structural defenses. We measured the physical defenses of 99 individual cactus plants in three 10 × 10 m quadrats centered on a woodrat midden. Quadrats were separated by at least 100 m. Cacti were identified as *Opuntia macrorhiza* × *O. polyacantha* hybrids, which are common throughout Utah (A. Dean Stock pers. comm.). For each plant, we measured the length of a terminal pad, as well as the length of the longest spine emanating from the terminal areole on that pad. Additionally, we determined the percentage of areoles that had spines.

Preference trials in captivity

We determined the collection preference, feeding preference, and feeding behavior of woodrats given access to different cactus types. Collection preference was measured by giving animals two hours to collect cactus from the arms of a T-maze. The type of cactus returned to the home cage was recorded as preferred. Feeding preference was measured by giving animals overnight access to two cactus types, and measuring the amount eaten of each type. Feeding behavior was observed by giving woodrats a spiny cactus overnight and inspecting the remains. For these experiments, we used three types of cacti: 'spiny' cacti were ones that were spiny in nature (>75% of areoles with spines) and left intact; 'de-spined' cacti were ones that were spiny in nature, but spines had been experimentally removed; 'non-spiny' cacti were ones that lacked extensive spines in nature (<20% of areoles with spines). All cacti were handled identically with gloves and metal forceps to reduce the likelihood of odor transfer from the experimenter to the cactus. All unmanipulated cacti (spiny or non-spiny) were placed on the lab bench next to cacti that were being 'de-spined', and so were exposed to similar environmental conditions before being presented to woodrats. To 'de-spine' cacti, the cacti were held with metal forceps and a wire cutter was used to clip spines at their base. We did not remove the small, hair-like, glochid spines, as these are present on 'non-spiny' cacti. Care was taken to not damage any of the green, photosynthetic tissue. The same animals were used in all trials with at least two weeks of time in between trials. All trials were conducted at the beginning of the animals' dark cycle, when woodrats are active. Woodrats were not under a food deprivation regime to prepare for trials, though were unlikely to have fed since the previous dark cycle. All experiments outlined below took place during from June – August 2013, meaning that animals captured at different time experienced different times in captivity. Our sample sizes were too low to test for effect of time in captivity on cactus consumption.

Woodrats naturally collect and cache their food material. Because plant tissue is being removed during collection, it represents herbivory from the plants' perspective. Therefore, we determined the collection preference of *N. albigula*. A T-maze was attached to the cages of woodrats for two hours. The T-maze consisted of a starting arm with dimensions of 78 × 12 cm, and two choice arms of 82 × 12 cm. Spiny and de-spined cacti were placed in each choice arm of the maze. The locations of spiny and de-spined cacti were alternated for each woodrat. After one hour, we documented which cactus type had been brought back to the animal's home cage. We conducted this test on eight *N. albigula* that were collected from nature. We used a one proportion Z-test to test for significance in selection preference. We also conducted this experiment on two individuals that were born in captivity to investigate whether this preference might be an innate. However, a sample size of two individuals was not sufficient for statistical analyses. These animals had only been exposed to cacti once before, in an experiment described below.

Feeding preference of *N. albigula* was measured by placing two cactus types in an animal's cage overnight and measuring the intake of each type. We conducted the following comparisons: spiny versus de-spined; and spiny versus non-spiny with eight woodrats for each test. A small section of each cactus pad was cut off to measure water content, and the wet mass of the cactus presented to the animals was recorded. Woodrats were allowed to feed on cacti for 12 h overnight. The next morning, the left over cactus material was removed from the cage and dried at 45°C. The amount of cactus provided was sufficient for animals to feed solely from one type and maintain body mass, and animals only consumed 47 ± 2% of total cacti provided. We calculated the proportion of the dry mass consumed of each type. We conducted a t-test to investigate whether the average proportion of spiny cactus consumed was different than 50%.

Last, we investigated whether *N. albigula* exhibited unique behavioral adaptation to feeding on cacti. We compared the feeding behavior of *N. albigula* to another species, the desert woodrat (*N. lepida*; collected from Lytle Ranch, Washington Co., UT, 37°07'N, 114°00'W, in May 2012), which does not specialize on cactus (n = 8 for each species). Each woodrat species was given a spiny cactus and we documented whether the animals clipped spines off of the cactus or not. Additionally, we conducted this trial with two individuals of *N. albigula* that were born in captivity and had never been exposed to cactus before. This experiment was the first time that these animals were exposed to cacti.

Nutrient composition

We compared the nutritional content of spiny (>75% of areoles with spines) and non-spiny (<20% of areoles with spines) cacti. Three or four individual plants were sampled from each of the three quadrats in which we measured variability in structural defenses, for a total of 11 individual plants of each type. Spines were removed from spiny cacti so that they did not influence nutritional measurements. Wet mass was recorded and samples were dried at 45°C until mass was constant to determine percent water. Total fiber (neutral detergent fiber; NDF) and cellulose/lignin (acid detergent fiber; ADF) were measured using a fiber analyzer. Percent nitrogen was

determined using stable isotope analysis described under 'Characterization of feeding' and multiplied by the standard nitrogen-to-protein conversion factor of 6.25 to generate an estimate of crude protein (Karasov and Martinez del Rio 2007). Oxalate concentration was determined using a previously established technique (Baker 1952).

Results

Characterization of feeding in nature

Stable isotope analysis revealed that *Neotoma albigula* at Castle Valley specialize on cactus. The isotope signatures in the hair of animals were similar to what would be predicted of a 100% cactus diet and were drastically different than the signatures of sage brush or juniper (Fig. 1).

Variability of structural defenses in nature

Cacti from the plots exhibited a great deal of variability in structural defenses in the wild. There was a significant correlation between cactus pad length and terminal spine length ($p = 0.0013$; Fig. 2a). However, a very small amount of variation was explained by this relationship ($R^2 = 0.10$). Cacti contained spines on roughly 60% of their areoles (mean 59%; median 64%; Fig. 2b). The range of this measurement was not normal (Shapiro–Wilk W test: $p = 0.004$) and was left-skewed.

Preference trials in captivity

Neotoma albigula strongly preferred to collect spiny cacti to experimentally de-spined cacti. During the choice trial, seven of eight wild-caught animals collected the spiny cactus pad

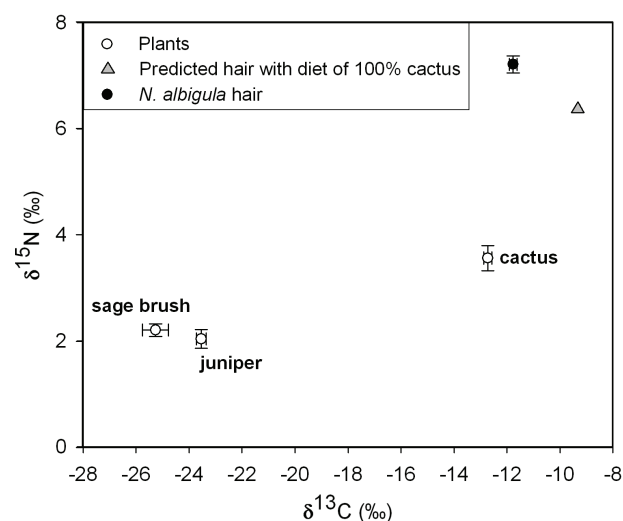


Figure 1. Values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from plant samples and hair of *N. albigula*. Isotope values for juniper *Juniperus osteosperma*, sagebrush *Artemisia* spp. and cactus *Opuntia macrorhiza* × *O. polyacantha* hybrids are shown in open circles. The grey triangle represents the predicted signature of woodrat hair if animals were consuming a diet of 100% cactus, using the diet-tissue fractionation rates measured in rabbits of 3.4‰ for $\delta^{13}\text{C}$ and 2.8‰ for $\delta^{15}\text{N}$ (Sponheimer et al. 2003a, b).

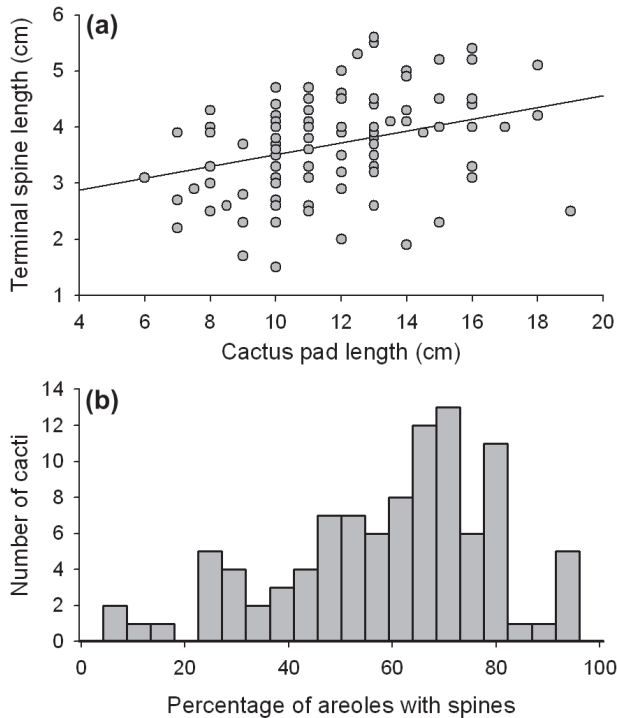


Figure 2. Variability of structural defenses in cacti *Opuntia macrorhiza* × *O. polyacantha* hybrids. (a) The relationship between cactus pad length and terminal spine length. The solid line represents a linear regression. (b) Histogram of the percentage of areoles with spines.

to their home cage. The only animal that did not exhibit this behavior moved a substantial amount of bedding to build a nest next to the spiny cactus within the T-maze (Supplementary material Appendix 1 Fig. A1) and thus was deemed to have selected the spiny cactus. Overall, wild-caught animals preferred to select spiny cactus for caching (Fig. 3; $Z = 2.83$, $p = 0.005$). Similarly, the two animals born in captivity brought spiny cactus pads back to their home cages. No animals ever collected the non-spiny cactus pads.

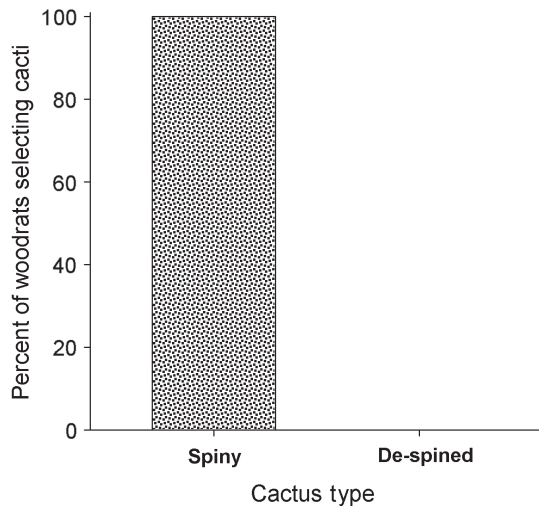


Figure 3. Results of collection choice trials with *N. albigula*. All animals selected the spiny cacti over the experimentally de-spined cacti. This difference was statistically significant using the Z-test.

Neotoma albigula also preferred to feed on spiny cacti compared to non-spiny cacti. When given extended access to spiny and naturally non-spiny cacti, woodrats significantly preferred feeding on the spiny cacti ($p = 0.016$; Fig. 4). However, this behavior was not a function of the spines per se because when animals had access to both spiny and experimentally de-spined cacti, there was no preference for either type ($p = 0.9$; Fig. 4). It should also be noted that woodrats clipped spines off of the spiny cacti in both trials.

A comparison of feeding behavior demonstrated that *N. albigula* are behaviorally adapted to feed on cacti. All *N. albigula* clipped spines at the base and were able to consume substantial amounts of cacti (Fig. 5). Individuals of *N. albigula* that were born in captivity also clipped off cactus spines, even though this experiment was their first contact with cactus. Conversely, none of the *N. lepida* tested exhibited this strategy. Rather, *N. lepida* left the spines intact and could only consume portions of the cactus pads (Fig. 5).

Nutrient composition

Nutritional analyses revealed several differences between the cacti types. The cacti types did not exhibit any difference in water content (Table 1). Spiny cacti contained significantly less total fiber than non-spiny cacti as measured by neutral detergent fiber, but there was no difference in cellulose or lignin as measured by acid detergent fiber (Table 1). Spiny cacti also contained $1.27 \times$ more crude protein and $1.14 \times$ more oxalate than non-spiny cacti (Table 1).

Discussion

Our study tested the efficacy of cactus spines as a structural defense against a specialist herbivore, the white-throated woodrat *Neotoma albigula*. We found that spines were

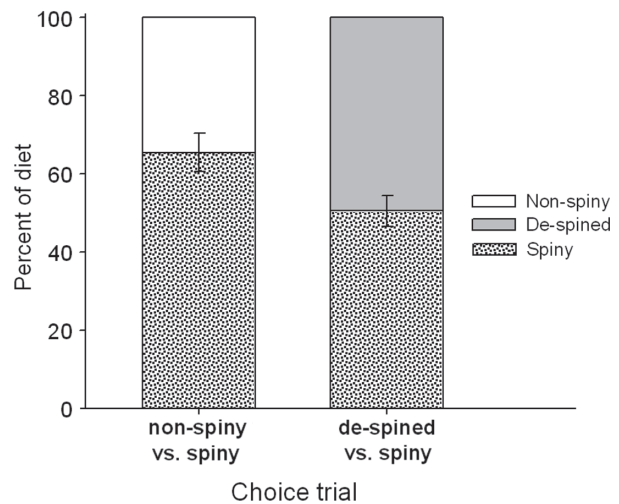


Figure 4. Results of feeding preference trials. Bars represent the mean \pm SEM. percent that each cactus type constituted of the animals overall food intake. Because this was a two-choice test, standard error values are identical for both choices, and thus only one error bar is plotted. There was no difference in preference between spiny cacti and experimentally de-spined cacti. Woodrats preferred spiny cacti to naturally non-spiny cacti.

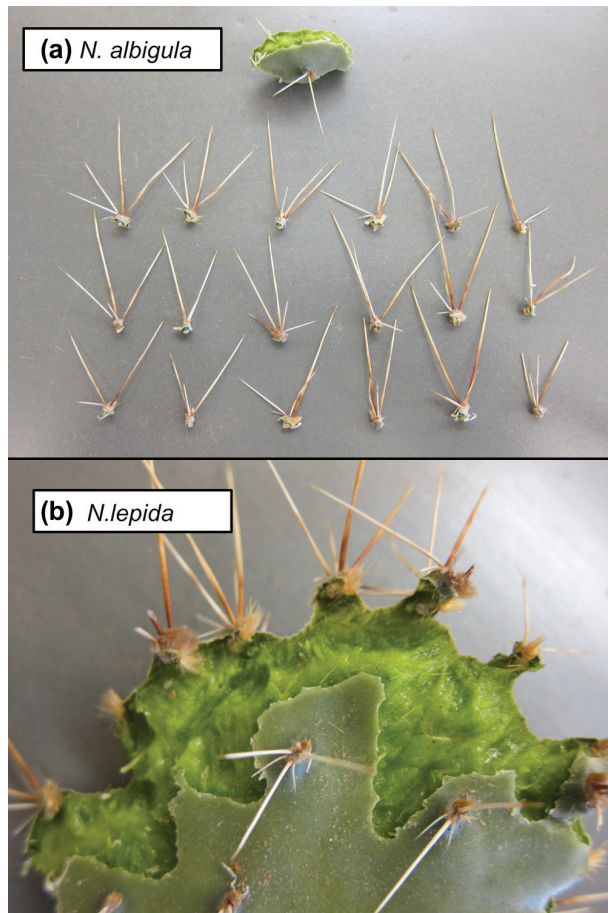


Figure 5. Representative food remains from (a) *N. albigula* and (b) *N. lepida* offered spiny cactus pads overnight. *Neotoma albigula* removed spines and were able to consume entire pads of cacti, thus the picture only shows the left over spines. *Neotoma lepida* did not remove spines, which often limited access to cactus flesh.

ineffective due to the behavioral adaptations of *N. albigula*. Interestingly, *N. albigula* preferred and selected spiny cacti over non-spiny cacti. Spiny cacti are likely selected for their higher protein content and lower fiber content. Thus, overall, the structural ‘defenses’ of spines appear to act as a proximate cue to attract a mammalian herbivore. We discuss these findings below in the context of ecological theory.

A number of studies, including ours, document wide variability in structural defenses among individual plants (Chavez-Ramirez et al. 1997, Cooper and Ginnett 1998). Structural defenses are hypothesized to be costly, and thus plants may divert resources to growth or reproduction in lieu of spines (Hanley et al. 2007). For example,

Table 1. Nutritional content of spiny and non-spiny cacti (*Opuntia macrorhiza* × *O. polyacantha* hybrids). n = 11 for each type. Water content is percent of wet mass. All others are percent of dry mass.

Measurement	Spiny	Non-spiny	p-value
Water content	78.9 ± 2.2	80.7 ± 2.2	0.60
Total fiber (NDF)	45.5 ± 1.9	57.0 ± 3.3	0.008
Cellulose/lignin (ADF)	9.4 ± 0.5	9.6 ± 0.5	0.74
Crude protein	5.2 ± 0.5	4.1 ± 0.2	0.04
Oxalate	1.49 ± 0.04	1.31 ± 0.05	0.01

Acacia drepanolobium exhibited decreases in spine length after the exclusion of herbivores (Young and Okello 1998). Plants may also experience tradeoffs with chemical defenses (Hanley et al. 2007). We did not find evidence of this tradeoff, as spiny cacti had higher concentrations of oxalate, their most common chemical defense. The suite of herbivores that cacti face may drive the variation in structural defenses in the population we studied. While spines are ineffective and actually attract woodrats, they may be effective against larger herbivores, or provide protection from heat or UV radiation (Lewis and Nobel 1977, Nobel 1978).

The white-throated woodrat exhibited a highly unique behavioral adaptation of clipping cactus spines to overcome structural defenses. This behavior has been previously reported for this species (Richardson 1943), but here we demonstrate that this behavior is not shared by all members of *Neotoma*. Further, this behavior was exhibited by two woodrats that were born in captivity and had never encountered cactus before, suggesting that this behavior is innate. Plant spinescence typically induces some behavioral responses in herbivores, such as reduced bite size (Wilson and Kerley 2003a). However, examples of behavioral adaptations in vertebrates for overcoming plant spinescence are rather rare. The manual dexterity of mountain gorillas allow them to engage in complex leaf-gathering skills to avoid plant spines (Byrne and Byrne 1993). The spine clipping behavior of *N. albigula* represents another unique behavioral adaptation to plant spinescence.

Notably, woodrats greatly preferred spiny cacti. In the collection test, all woodrats chose spiny cacti over experimentally de-spined cacti. Further, in the feeding trial they preferred spiny cacti to naturally non-spiny cacti. Cactus spines may be used by woodrats as a defense against predators. *Neotoma albigula* regularly lines the entrances of their middens with cactus spines (Torregrossa and Dearing 2009), and woodrats that incorporate *Opuntia* into their nests exhibit higher survival rates in the wild (Smith 1995).

Nutritional analyses revealed a number of differences between cactus types that may also explain these preferences. Spiny cacti had significantly higher concentrations of the secondary compound oxalate. It may seem perplexing that woodrats would prefer cacti with higher oxalate. However, *N. albigula* can consume diets of 9% oxalate without any adverse effects (Justice 1985). Thus, the oxalate concentrations of cacti (1.3–1.5%) likely do not present a large enough challenge to determine foraging behavior. Spiny cacti also had lower concentrations of total fiber, perhaps indicative of a higher concentration of easily digestible, non-structural carbohydrates. Last, spiny cacti contained absolutely 1% more crude protein compared to non-spiny cacti. This translates into a 27% relative difference, which is a relative difference that is detectable by woodrats (Post 1993). Other herbivores are known to forage according to protein content of plants (Moore et al. 2010, Frye et al. 2013), and thus this nutrient difference likely drives the preference for spiny cacti. The protein content of cacti is exceptionally low, much lower than the minimum protein requirements of most herbivorous mammals (Karasov 1982, Robbins 1993). However, woodrats exhibit exceptionally low minimum nitrogen requirements compared to other eutherian mammals, and

are able to maintain nitrogen balance on diets containing less than 1% nitrogen (6.25% crude protein) (Dearing et al. 2005b). It would be interesting to compare metrics of woodrat performance (nitrogen balance, fiber digestibility, etc.) when feeding on each cactus type.

Interestingly, the 'defensive' spines of cacti appeared to act as a proximal cue in attracting selection by woodrats. Woodrats chose spiny cacti over experimentally de-spined cacti in the selection experiment, even though the tissues of these plants were identical and thus lacked any nutritional differences. Thus, white-throated woodrats probably do not forage exclusively based on the chemical or nutritional content of plants (known as 'nutritional wisdom') (Stephens and Krebs 1986). However, it should be noted that woodrats are able to discriminate against diets of varying nutrient quality and therefore do possess some 'nutritional wisdom' (Post 1993). Instead, our results lend more support to the 'rule-of-thumb' hypothesis of foraging (Stephens and Krebs 1986, Cassini 1994). For example, predators are often unable to sample the nutritional content of their prey and instead select the largest prey as a likely indicator of profitability (Stephens and Krebs 1986). Likewise, herbivores may utilize obvious cues to select plant material, such as size or color (Cassini 1994). Various invertebrate herbivores use chemical, tactile and visual 'rule-of-thumb' to select hosts plants (Rojas et al. 2003), however examples of these in vertebrates are remarkably rare. Our results support the 'rule-of-thumb' hypothesis, such that woodrats selecting spiny cacti are supplied with a diet lower in fiber and higher in nitrogen. This result is one of the very few examples of vertebrate herbivores following 'rules-of-thumb', though other herbivores are likely to follow them (Cassini 1994).

It is interesting that woodrats showed a strong preference for spiny over de-spined cacti in the T-maze, but no preference in the overnight experiment. Woodrats clipped off cactus spines themselves in the overnight experiment, essentially causing both types to be identical. Thus, we believe that cactus spines are important for collection preference in the wild, given that woodrats do not to consume plants in situ, but collect them for subsequent consumption. The feeding preference for spiny cacti over non-spiny cacti is likely driven by the nutritional differences between the two types. Thus, we hypothesize that woodrats use spines as a visual cue, and a 'rule of thumb' when collecting plant material in the environment. However, they still maintain 'nutritional wisdom' that allows them to select higher quality forage within their middens.

We cannot fully exclude the possibility of other cues that woodrats may use to select cacti. For example, *Opuntia* cacti are known to release volatile compounds (Wright and Setzer 2014), especially in response to herbivory (Woodward et al. 2012). Thus, volatile compounds may have differed across groups of cacti in our experiments and influenced woodrat selection. However, all cacti were handled identically in our experiments, and we took care not to damage the photosynthetic tissue of the plants during the de-spining process. Many herbivores also use visual cues, such as plant color, reflectance, or shape to select plants to feed on (Prokopy and Owens 1983). We did not compare these characteristics between spiny and non-spiny cacti, though we find it unlikely that they contribute largely to cacti selection.

Woodrats exhibited a strong preference for spiny cacti over experimentally de-spined cacti, even though both these cacti types shared similar visual characteristics given that they were all spiny to begin with.

The spines of cacti in Castle Valley likely evolved to deter herbivores, but instead attract a specialist herbivore. Thus, these plant 'defenses' represent an evolutionary irony, a relatively common phenomenon in biology that allows predators, parasites, or herbivores to co-opt signals to select prey, hosts or plants. For example, plant volatile chemicals that often serve as defenses can serve as cues to attract some lepidopteran herbivores (Bruce et al. 2005), mammalian herbivores (Bedoya-Pérez et al. 2014), and even parasitic plants (Runyon et al. 2006). Additionally, predatory bats (Tuttle and Ryan 1981) and parasitoid wasps (Cade 1975) use the mating calls of prey for determining their location. Last, seed-predating rodents may consume the fleshy fruit of plants and destroy the seeds meant for seed dispersers (Samuni-Blank et al. 2013). Our results represent another example of evolutionary irony. However, in our system as well as others, it is difficult to determine the relative fitness costs and benefits of these traits.

Overall, our results expand the knowledge of herbivore counter-adaptations of mammalian herbivores to structural defenses, foraging theory of mammalian herbivores, and evolutionary irony. Though specialist vertebrate herbivores are relatively rare (Shipley et al. 2009), they may represent unique study systems in which to further our understanding of these areas.

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Supplementary material (available online as Appendix oik.02004 at www.oikosjournal.org/readers/appendix). Appendix 1.