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ABSTRACT

Dietary specialization is thought to be rare in mammalian herbivores as a result of either a limitation in their detoxification system to metabolize higher doses of plant secondary compounds or deficiencies in nutrients present in a diet composed of a single species of plant. *Neotoma macrotis* is an oak specialist, whereas *Neotoma lepida* is a dietary generalist when sympatric with *N. macrotis*. We hypothesized that *N. macrotis* would have a higher tolerance for and digestibility of oak. We determined the two species' tolerances for oak by feeding them increasing concentrations of ground oak leaves until they could no longer maintain body mass. The highest concentration on which both species maintained body mass was 75% oak. There were no differences between the species in their abilities to digest dry matter, nitrogen, or fiber in the oak diets. The species' similar tolerances for oak were probably due to their similar abilities to digest and potentially assimilate the ground oak leaves.

Introduction

The diets of herbivorous mammals are usually low in nitrogen and high in fiber and contain potentially toxic plant secondary compounds (PSC). Yet, herbivory is a common dietary strategy in a number of mammalian families, and mammalian herbivores possess many anatomical, physiological, and behavioral adaptations to consume plants. Most mammalian herbivores deal with nutrient limitations and PSCs by being dietary generalists and eating from a variety of different plants either within the same foraging bout or from different foraging bouts (Freeland and Janzen 1974; Westoby 1978). Few mammalian herbivores are dietary specialists using a single plant species for more than 70% of the diet (Freeland 1991).

Within the genus *Neotoma* (woodrat), three species have evolved dietary specialization on three different plants. *Neotoma stephensi* is a specialist on one-seeded juniper (*Juniperus monosperma*; Vaughn 1982; Dial 1988). Populations of *Neotoma lepida* in the Mojave Desert specialize on creosote bush (*Larrea tridentata*; Cameron and Rainey 1972; Karasov 1989). Last, *Neotoma macrotis* (formally a subspecies of *Neotoma fuscipes* Matocq 2002) is a specialist on oak (*Quercus agrifolia*) in the western coastal Santa Ana Mountains (Atsatt and Ingram 1983). Previous research suggests that *N. stephensi* and *N. lepida* are able to specialize on their host plant because they have a superior ability to detoxify the PSCs of the host plant (*N. stephensi*: Dearing et al. 2000; Sorensen and Dearing 2003; Green et al. 2004; Lamb et al. 2004; Sorensen et al. 2004; Skopec et al. 2007; *N. lepida*: Mangione et al. 2000, 2001; Lamb et al. 2001). Dietary specialization of *N. macrotis* has been less well studied; it is not known whether *N. macrotis* is able to specialize on oak because it has a specialized detoxification system to metabolize the PSCs in oak or adaptations to overcome nutrient limitations of a high oak diet. Oak is a challenging diet because it is high in phenolics (7% by dry weight) and fiber (41% by dry weight) as well as low in nitrogen (1.4%; Table 1). Yet, *N. macrotis* consumes oak as 85% or more of its diet, while a sympatric population of *N. lepida* consumes less oak in the field (39%; Cameron and Rainey 1972). In a previous laboratory trial, *N. lepida* could not maintain body mass on an oak diet (Atsatt and Ingram 1983). Atsatt and Ingram (1983) suggested that *N. lepida* were unable to thrive on the oak diet because of its high fiber and/or tannin content. A recent report on the detoxification abilities of these two species under natural conditions is consistent with the idea that the oak specialist *N. macrotis* (*N. fuscipes*) processes higher levels of toxins in its diet (Dearing et al. 2006). When both species were administered hexobarbital, *N. macrotis* cleared the drug significantly faster than did *N. lepida*. Also, under laboratory conditions, *N. macrotis* and *N. lepida* induce different detoxification enzymes in response to an oak diet (Haley et al. 2007).

We compared the tolerances of captive *N. macrotis* and *N. lepida* to oak as well as their ability to digest the nitrogen and fiber present in oak. We fed both species diets with increasing levels of oak and measured their dry matter intake (DMI), body

Table 1: Nutrient and chemical composition of the diets

Diet Component	Diet (% Oak)					
	0	10	25	50	75	100
Nitrogen	2.3	2.2	2.0	1.8	1.6	1.4
Acid detergent fiber	25.3	29.4	30.9	32.5	35.8	40.8
Total phenolics	.4	1.1	2.2	3.9	5.6	7.3

Note: Diet components are shown as percent of diet. See "Material and Methods" for description of techniques used to quantify diet components.

mass, as well as the dry matter, fiber, and apparent nitrogen digestibilities (DMD, FD, ND) on each diet. On the basis of previous studies (Atsatt and Ingram 1983; Dearing et al. 2006; Haley et al. 2007), we predicted that *N. macrotis* would have a higher tolerance for oak diets and greater digestibilities than *N. lepida*. We feel that our gradual transition diet is more ecologically and physiologically relevant since in the field, woodrats are not forced to eat either only oak or no oak and can acclimate themselves to oak if they choose.

Material and Methods

Study System

Neotoma macrotis and *Neotoma lepida* were trapped near Caspers Wilderness Park, San Juan Capistrano, California, and transported to the University of Utah Department of Biology's Animal Facility. All animals were screened for hantavirus before experimentation. Woodrats were housed in individual cages (48 cm × 27 cm × 20 cm) with pine shavings on a 12L : 12D cycle at 28°C and with a relative humidity of 15% for at least 6 mo before experiments. The woodrats were fed high-fiber rabbit chow (Harlan Teklad formula 2031) and water ad lib. All experimental procedures involving woodrats were approved by the University of Utah's Institutional Animal Care and Use Committee (protocol no. 04-02012).

Dietary Treatments and Analysis

The oak leaves used in the dietary treatments (*Quercus agrifolia*) were collected from ∼10 trees at woodrat trapping sites and frozen at −20°C until use. The oak foliage was ground in a Waring blender (model CB-5) until it passed through a 1.0-mm screen. Diets were ground because woodrats forage selectively to minimize fiber intake (Smith 1995). The diets were made daily to minimize the oxidation of the tannins. The diet treatments contained increasing percentages of ground oak mixed with ground high-fiber rabbit chow (Harlan Teklad 2031). The diets were comprised of 0%, 10%, 25%, 50%, 75%, and 100% oak (wet weight). The average dry matter content of the collected ground oak was 44%. No additional water was added when mixing the diets.

The dry matter contents of the diets were determined by placing 10-g samples of each diet fed each day in a drying oven at 50°C. Total phenolics were extracted from the oak diets by

homogenizing the diet with 85% methanol with a Polytron homogenizer (Brinkman Polytron; Torti et al. 1995) and assayed for total phenolics using the Folin-Coicalteu method (Singleton and Rossi 1965) and a tannic acid standard (Sigma-Aldrich). The nitrogen content of the diets was measured via a micro-Kjeldahl digestion followed by a phenol-hypochlorite colorimetric determination of ammonia (Weatherburn 1967). The fiber contents of the diets were quantified using an Ankom fiber analyzer 200/200 (Ankom, Fairport, NY) and the acid detergent fiber method (Van Soest and Jones 1988).

Experimental Protocol

During the experiments, animals were housed in plastic metabolic chambers (Lab Products, no. 2100R) that allowed for the complete separation of urine and feces. A total of 10 animals per species (five males and five females) were included in the feeding trial. Food intake, body mass, and fecal output were measured daily. If animals lost more than 10% of their initial body mass, they were removed from the trial. Animals were fed diets with increasing concentrations of oak sequentially: 0% oak for 3 d, 10% oak for 9 d, 25% oak for 3 d, 50% oak for 3 d, 75% oak for 3 d, 100% oak for 3 d. The initial diet of oak (10%) was fed for a longer period of 9 d to fully acclimate animals to oak (Skopec et al. 2004; Shimada et al. 2006). We gradually increased the percentage of oak in the diet to give the woodrats time to increase the production of salivary tannin-binding proteins, mucus excretion in the gut, and/or numbers of tannin-degrading bacteria in the hindgut, all of which are physiological responses to tannins in a number of mammals (Glick and Joslyn 1969; Mitjavila et al. 1977; Mehansho et al. 1983; Osawa 1991; Jansman et al. 1995; Skopec et al. 2004; Shimada 2006).

Fecal Analysis

Fecal samples were dried at 50°C and reweighed to determine dry matter content. The dried fecal samples were then ground using a mortar and pestle and partitioned for nitrogen and fiber analysis. The nitrogen and fiber content of the feces was analyzed using the same methods described above for the diet.

Digestibility Calculations

We estimated the DMD, ND, and FD on a 24-h basis. Digestibility was calculated for each component as [(grams intake − grams output)]/grams intake.

Survivorship

The period of time that the two species of woodrats remained in the trial before losing more than 10% of body mass was calculated using Kaplan-Meier survival analysis in SYSTAT 10 (Wilkinson and Coward 2000). The mean survival time for each species was compared using a log rank test in SYSTAT 10

(Wilkinson and Coward 2000). Survival analysis methods are used to compare the time to any discrete event, and while death is a common end point, other end points are often used (Lee and Wang 2003). This study used a loss of 10% body mass.

Cecum Volumes

To determine whether *N. macrotis* has a greater ability to digest fiber and therefore specialize on oak, we measured the size of the cecum in both species in a separate feeding trial (Van Soest 1994). *Neotoma macrotis* ($n = 15$) and *N. lepida* ($n = 12$) were fed either the control diet (ground high-fiber rabbit chow) or an oak diet (70% oak). Food intakes and body mass were measured daily. Animals were fed the control diet (*N. macrotis*: $n = 8$; *N. lepida*: $n = 6$) for 10 d. Animals fed the oak diet (*N. macrotis*: $n = 7$; *N. lepida*: $n = 6$) were fed the control diet for 3 d, 25% oak diet for 3 d, 50% oak diet for 3 d, and 70% oak diet for 3 d. At the end of the 12 d, animals were killed via CO_2 asphyxiation, and their digestive tracts were removed and placed in 10% formalin. The small and large intestines were removed from the cecum at the ileocecal valve and cecocolic junction, respectively. Water displacement was used to estimate cecum volume to the nearest milliliter.

Statistical Analysis

DMI, body mass, and DMD, ND, and FD were analyzed as 3-d averages. For the 10% oak diet that was fed for 9 d, we used the average of the last 3 d. Only data from those animals that finished the entire trial were used (*N. macrotis*: $n = 5$; *N. lepida*: $n = 5$). DMD, ND, and FD were normalized by an arcsine–square root transformation. Data were analyzed by repeated-measures ANOVA with species and diet as factors using SYSTAT (Wilkinson and Coward 2000). Body mass was a significant covariate for DMI; therefore, DMI was analyzed as DMI per gram of body mass. Differences between individual means were determined by Tukey's honestly significant differences (HSD) test. Body mass was also a significant covariate for cecum volume; therefore, cecum volume was analyzed as cecum volume per gram of body mass by ANOVA with species and diet as factors using SYSTAT (Wilkinson and Coward 2000). Differences between individual means were determined by Tukey's HSD. All data are expressed as means $\pm$ SE.

Results

Dry Matter Intake and Body Mass

While the two species did not differ in starting body mass ($P = 0.132$), body mass was a significant covariate for DMI ($P < 0.001$); therefore, DMI was analyzed as DMI per gram body mass. DMIs per gram body mass for both species were highest on the 50% and 75% oak diets and lowest on the 0% and 100% oak diets (Fig. 1A). *Neotoma macrotis* had a greater body mass on the 25% and 50% oak diet compared with the 0% oak diet and lost an average of 5% of their initial body mass on the
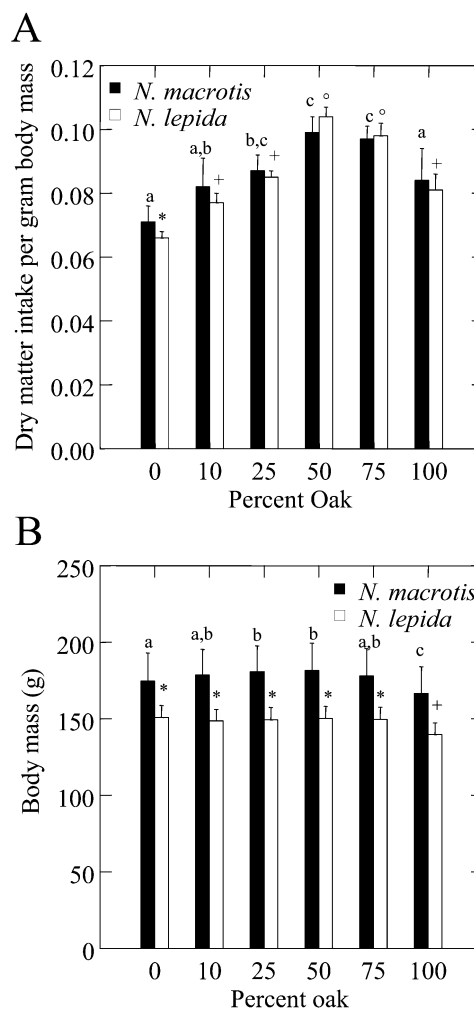

Figure 1. Mean dry matter intake per gram body mass per day (*A*) and body mass (*B*) of *Neotoma macrotis* and *Neotoma lepida* by the percentage of oak in the diet. Dry matter intake and body mass were not significantly different between the species on any diet treatment. Letters denote means that are significantly different ($P < 0.05$) within *N. macrotis*, and symbols (*asterisks*, *plus signs*, *degree signs*) denote means that are significantly different ($P < 0.05$) within *N. lepida* as determined by Tukey's honestly significant differences test.

100% oak diet (Fig. 1B). *Neotoma lepida* did not gain body mass on any diet and lost an average of 7% of initial body mass on the 100% oak diet. There was no significant difference between the species on any diet treatment in body mass ($F_{1,8} = 2.236$, $P = 0.173$) or DMI ($F_{1,8} = 0.053$, $P = 0.833$).

Dry Matter Digestibility

DMD decreased for both species on the 100% oak diet (Fig. 2A). While there was no overall species difference in DMD ($F_{1,8} = 6.41$, $P = 0.24$), DMD in *N. macrotis* started to decrease with the addition of 25% oak to its diet, while *N. lepida* did not have a reduced DMD until the 75% oak diet (Fig. 2A).
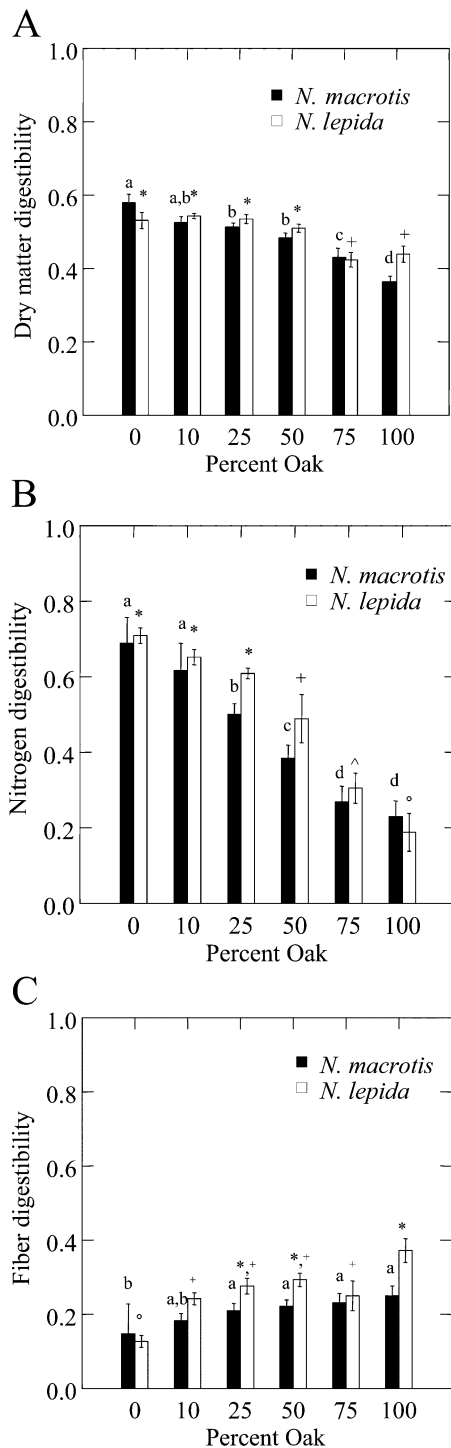
Figure 2. Digestibility parameters of diets fed to *Neotoma macrotis* and *Neotoma lepida* by the percentage of oak in the diet. Dry matter digestibility (*A*), nitrogen digestibility (*B*), and fiber digestibility (*C*) were not significantly different between the species on any diet. Letters denote means that are significantly different (*P* < 0.05) within *N. macrotis*, and symbols (*asterisks, plus signs, degree signs, carets*) denote means that are significantly different (*P* < 0.05) within *N. lepida* as determined by Tukey's honestly significant differences test.

Nitrogen Digestibility

Apparent ND also decreased in both species as the percentage of oak in the diets increased (Fig. 2*B*). For *N. macrotis*, the decrease in ND began with the 25% oak diet, while ND in *N. lepida* did not decrease until the 50% oak diet. There was not a significant species effect on ND ($F_{1,8} = 180.073$, $P = 0.537$).

Fiber Digestibility

FD increased in both species on the oak diets compared with the 0% oak diet (Fig. 2*C*). *Neotoma macrotis* showed no difference in FD on any of the oak diets (10%–100%), while *N. lepida* had an increased FD on the 100% oak diet compared with the 10% oak diet. There was a trend toward a difference in FD between species ($F_{1,8} = 65.1$, $P = 0.099$), with *N. lepida* having higher FD on all diets except for the 0% oak diet.

Survivorship

Both species ended with the same survival rate of 0.50 (Fig. 3). Mean survival times were not significantly different ($\chi^2_1 = 0.193$, $P = 0.660$). Both species had mean survival times that fell within the period that the 75% oak diet was fed (*N. macrotis*: 20.7 d; *N. lepida*: 21.3 d).

Cecum Volume

Neotoma lepida had a higher mean cecal volume per gram body mass on the 70% oak diet (Fig. 4). *Neotoma macrotis* also had larger cecal volumes when fed a 70% oak diet compared with a 0% oak diet, but the difference was not significant. There were no differences between the species on either diets ($F_{1,23} = 1.366$, $P = 0.254$).

Discussion

Dietary specialization is thought to be rare in mammalian herbivores because of a limitation in their detoxification system to metabolize high doses of PSCs present or nutrient deficiencies in a diet composed of a single species of plant (Freeland and Janzen 1974; Westoby 1978). *Neotoma macrotis* is a documented oak specialist, while sympatric populations of *Neotoma lepida* have a much greater diet breadth (Cameron and Rainey 1972; Atsatt and Ingram 1983). We compared *N. macrotis* and *N. lepida*'s tolerance and ability to digest oak to determine the mechanism by which *N. macrotis* is able to specialize on oak. Surprisingly, we found that not only did both species have similar tolerances for oak but also they had similar abilities to digest the nitrogen and fiber present in the oak. We discuss the ability of *N. macrotis* and *N. lepida* to deal with oak diets, why our results may be different from previous studies, and why *N. lepida* is not an oak specialist in the wild.

Oak Tolerance

Despite the fact that *N. macrotis* and *N. lepida* feed on oak at different levels in the wild, they had similar tolerances to oak in captivity. We defined tolerance as the concentration of oak that each species was able to consume and maintain body mass. Both *N. macrotis* and *N. lepida* maintained body mass on increasing concentrations of oak until a 100% oak diet. *Neotoma macrotis* lost an average of 5% of their initial body mass, while *N. lepida* lost an average of 7% on the 100% oak diet (Fig. 1*B*). The body mass loss for both species is explainable by their decrease in DMI on the 100% oak diet compared with the 75% oak diet. Both species increased DMI as the concentration of oak in the diets increased until the 75% oak diet. This increase in DMI is likely due to the higher fiber content and therefore lower energy density of oak than rabbit chow (Fig. 1*A*; cf. 0% diet and 100% diet). However, animals decreased DMI at 100% and exhibited mass loss. Also, both species had mean survival times that fell within the period that the 75% oak diet was fed (*N. macrotis*: 20.7 d; *N. lepida*: 21.3 d). Therefore, both species can tolerate diets containing 75% oak.

Oak Digestibility

There was no difference in the two species' ability to digest the oak diets (Fig. 2), although increasing amounts of oak altered the digestibility of the diet. The DMD and ND of oak diets decreased with increasing concentrations of oak, while FD increased with increasing concentrations of oak. The observed decrease in ND is consistent with findings from other studies with tannin diets. Either the tannins present in oak may combine with the nitrogen in the oak, making it unavailable for digestion (Bernays et al. 1989), or the decrease in ND may be

Figure 4. Cecal volumes of *Neotoma macrotis* and *Neotoma lepida* on a control versus oak diet. The control diet was ground high-fiber rabbit chow, and the oak diet was 75% ground oak and 25% ground high-fiber rabbit chow. There was no difference between the species on either diet treatment, but there was a significant difference ($P < 0.05$) between the cecal volume of *N. lepida* on the control versus oak diet.

due to increased endogenous losses of nitrogen that occur in response to tannins in the diet (Glick and Joslyn 1969; Mitjavila et al. 1977; Jansman et al. 1995; Skopec et al. 2004). The DMD decreased as the concentration of oak increased because oak has more fiber than the background diet of rabbit chow. Even though fiber was more digestible at higher concentrations, the increase in FD did not account for the increased concentration of fiber in the diet.

FD was the only parameter where the difference between the two species was almost significant. *Neotoma lepida* had ~25%
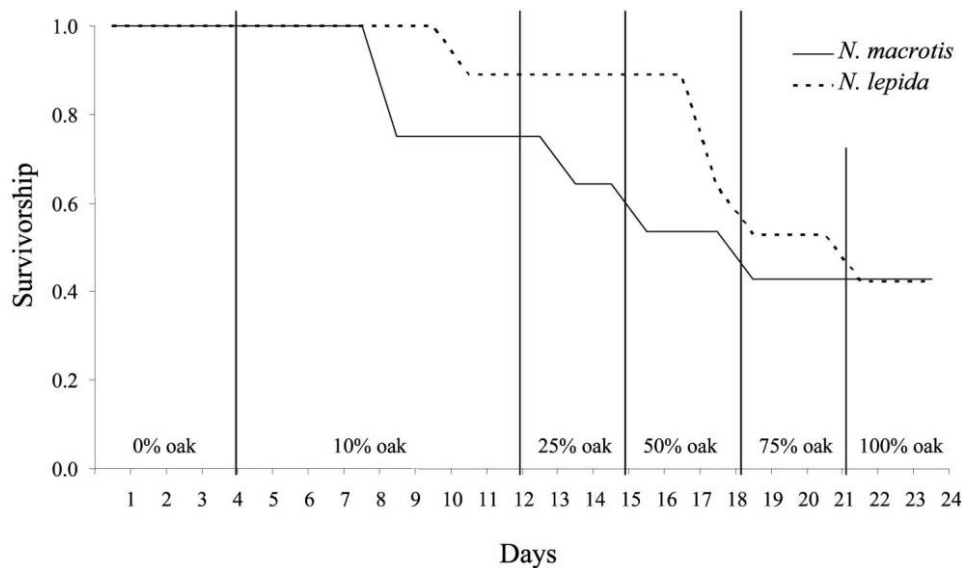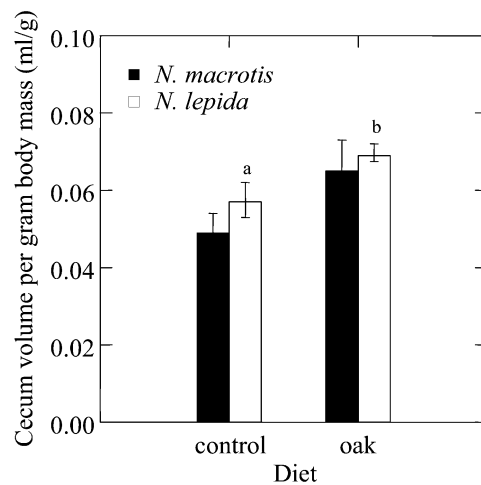
Figure 3. Survivorship of *Neotoma macrotis* and *Neotoma lepida* in the oak tolerance trial. Woodrats were removed from the experiment when they lost more than 10% of their initial body mass.

higher FD than did *N. macrotis* on the 100% oak diet ($P =$ 0.099). *Neotoma lepida*'s increased ability to digest the fiber present in oak might be due to a larger cecum, the primary site of fermentation. *Neotoma lepida* but not *N. macrotis* increased the size of their cecum in response to an oak diet (Fig. 4). *Neotoma lepida*'s increased ability to digest the fiber in the oak diet did not lead to an increased assimilation efficiency of the oak, since *N. lepida* and *N. macrotis* lost a similar amount of body mass on the 100% oak diet (Fig. 1*B*).

That *N. macrotis* and *N. lepida* did not differ in either their tolerances to oak or their abilities to digest oak is in direct conflict with both field observations and a previous laboratory study. Cameron (1971) estimated the oak contribution of the natural diets of sympatric *N. lepida* and *N. macrotis* to be 47% and 83%, respectively, on the basis of stomach content analysis. However, field data provide ecologically relevant information on what an animal chooses to consume and not necessarily on what an animal is able to eat. It is possible that although *N. lepida* appears able to survive on a diet of a much higher percentage of oak, it may not do so in the wild because of the presence of alternative plants, such as cactus, in its environment.

The laboratory feeding trial of Atsat and Ingram (1983) reported results that are drastically different from those presented here. When Atsatt and Ingram (1983) compared *N. macrotis* and *N. lepida* on an oak diet, *N. lepida* was unable to maintain body mass on a diet of 100% oak leaves; furthermore, *N. lepida*'s DMI was half that of *N. macrotis*. There were two major differences between our study and that by Atsatt and Ingram (1983). First, we increased the concentration of oak in the diet gradually, whereas Atsatt and Ingram (1983) switched the woodrats from a 0% to a 100% oak diet. Second, we fed the woodrats ground oak leaves, while Atsatt and Ingram fed whole leaves.

We gave the animals a 9-d acclimation period on the 10% oak diet, because some animals cannot consume a high-tannin diet immediately (Shimada et al. 2004, 2006). Increased production of salivary tannin-binding proteins, increased mucus excretion in the gut, and/or increased numbers of tannin-degrading bacteria in the hindgut are all physiological responses to tannins in a number of mammals (Glick and Joslyn 1969; Mitjavila et al. 1977; Mehansho et al. 1983; Osawa 1991; Jansman et al. 1995; Shimada 2006; Skopec et al. 2004). If tannins are not present in the diet, many mammals decrease the production of salivary tannin-binding proteins and mucus excretion in the gut, because they lead to significant fecal losses of endogenous nitrogen (Glick and Joslyn 1969; Mitjavila et al. 1977; Jansman et al. 1995; Skopec et al. 2004). Also, if tannins are not present in the diet, the population levels of tannin-degrading bacteria may decrease in the hindgut because of lack of substrates (Osawa 1991; Shimada et al. 2006). It is possible that since *N. macrotis* is an oak specialist, constitutive levels of tannin-binding proteins are high enough to consume an oak leaf diet without an acclimation period, while *N. lepida*'s constitutive levels of tannin-binding proteins are too low and they need an acclimation period to upregulate the aforementioned physiological adaptations.

The second major difference between our study and that by Atsatt and Ingram (1983) is that we fed ground oak leaves while they fed whole oak leaves. Although whole oak leaves are perhaps more ecologically relevant, we wanted to make sure there were no between-species differences in nutrient intake, which could occur with whole oak leaves because of species' differences in preference (i.e., selection among leaves or leaf parts) and processing (i.e., stripping and mastication of leaves). It is possible that *N. macrotis* is better at processing the oak leaves and therefore can reduce the tough oak leaves to a smaller particle size needed for optimal digestion. Particle size has a large effect on FD (Van Soest 1994). If *N. lepida* is not able to efficiently process whole oak leaves, they may suffer reduced fiber digestion, and this may restrict consumption of a diet high in oak in nature. Comparing both species on ground and whole oak leaves would reveal whether differences in processing ability result in differences in digestibility of oak. However, one would need to control for nutrient intake and sorting differences.

Neotoma lepida *an Oak Specialist?*

On the basis of our results, it seems that *N. lepida* could consume enough oak in the wild to be considered an oak specialist, yet their highest recorded intake in the wild is 65% (Cameron 1971). Interestingly, selection for a 65% oak diet by *N. lepida* occurred in allopatry instead of sympatry with *N. macrotis*; habitats and diet choices were similar in these comparisons. We therefore speculate that interspecific competition may limit *N. lepida*'s oak intake. In direct competition experiments *N. macrotis* always dominates *N. lepida* (Cameron 1971). Thus, if oak is the preferred food of *N. macrotis*, it may competitively exclude *N. lepida* from consuming it. Alternatively, the way in which *N. macrotis* feeds on oak in the field may increase the PSC content or decrease the nutritional quality of oak, thereby reducing the attractiveness of oak to *N. lepida*. Indirect competition between specialist and generalist herbivores mediated by specialists altering plant traits has been demonstrated in both marine invertebrates and insects (Kaplan and Denno 2007; Long et al. 2007).

Another possibility is that the tannins present in oak, while effective feeding deterrents, may not be acutely toxic. Many of the toxic effects of tannins are actually chronic effects (Bernays et al. 1989) and therefore may not have played a role in our relatively short-term feeding trial. *Neotoma macrotis* could still have a superior ability to detoxify the tannins present in oak, allowing them to negate the potential long-term toxicity of the tannins (Dearing et al. 2006). Longer-term feeding trials (>30 d) are necessary to determine this possibility.

Our study found that both species had a similar tolerance and ability to digest oak in captivity and that neither the nutrient limitation nor detoxification limitation theory explains why *N. lepida* acts as a dietary generalist when it is sympatric

with *N. macrotis*. There are a number of factors that could explain why *N. macrotis* is an oak specialist while sympatric populations of *N. lepida* act as dietary generalists. *Neotoma macrotis* may have a superior ability to sort or process whole oak leaves than *N. lepida*, they may be able to outcompete *N. lepida* for oak, or they may have a better ability to detoxify the tannins in oak and prevent chronic toxicity. Differences in mastication and competitive exclusion are two possible explanations that are not typically tested in studies of dietary specialization but that, in *N. lepida*, may be as important as or more important than nutrients or toxins in limiting their ability to specialize on oak when sympatric with *N. macrotis*.

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