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Effects of Consumption of Juniper (*Juniperus monosperma*) on Cost of Thermoregulation in the Woodrats *Neotoma albigula* and *Neotoma stephensi* at Different Acclimation Temperatures

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ABSTRACT

A study was done to test whether toxic plants that occur naturally in the diet affect thermoregulation in mammalian herbivores. The woodrats *Neotoma albigula* and *Neotoma stephensi* both consume juniper (*Juniperus monosperma*), a plant with high levels of toxic compounds. Body temperature (T_b), basal metabolic rate (BMR), and the minimum cost of thermogenesis (C_{min}) were measured for both species on control and juniper diets following warm (25°C) and cold (18°C) acclimation. In *N. albigula*, diet had no uniform effect on T_b , BMR, or C_{min} , but diet \times acclimation-temperature interaction effects on T_b and C_{min} were highly significant ($P < 0.005$). For thermoregulation at 15°C, juniper consumption increased the metabolic cost for warm-acclimated *N. albigula* by 50% but decreased the metabolic cost in cold-acclimated *N. albigula* by 24%. In *N. stephensi*, diet significantly affected T_b and C_{min} ($P < 0.05$), but there were no significant diet \times acclimation-temperature interaction effects. For thermoregulation at 15°C, juniper consumption increased the metabolic cost for warm-acclimated *N. stephensi* by 33% but had no significant effect on metabolic cost in cold-acclimated *N. stephensi*.

Introduction

For mammals, the energetic cost of maintaining a high constant body temperature in a cold environment can be very high. Small

mammals in particular lose heat easily to the environment because they have a high surface-area-to-volume ratio and because physical constraints limit the insulative thickness of fur (Schmidt-Nielsen 1993). To maintain a high body temperature in the cold, small mammals typically must rely on an increase in metabolic heat production (Hyvarinen 1994). During the winter, the elevated energy demands of thermoregulation in combination with reduced food availability make energy a limited resource. To conserve energy during the winter, many mammals have evolved endogenous physiological mechanisms to minimize thermoregulatory costs by either increasing insulation or reducing body temperature (i.e., torpor and hibernation; Nedergaard and Cannon 1990; Geiser and Ruf 1995). However, exogenous factors that may influence thermoregulatory costs also exist and either may impose additional thermoregulatory stresses during the winter or may be exploited by animals to facilitate thermoregulation.

One exogenous factor that may influence thermoregulatory physiology is the presence of toxins in the diet. Bozinovic and Novoa (1997) found that tannic acid, a common plant secondary compound, increases the metabolic cost of thermoregulation in two rodent species, the degu (*Octodon degus*) and the leaf-eared mouse (*Phyllotis darwini*). Fescue toxicosis, a pathological condition of grazing animals caused by grasses infected with the endophytic fungus *Acremonium coenophialum*, reduces the rate of heat loss because various alkaloids produced by the fungus act as vasoconstrictors and inhibit blood flow to the skin (Oliver et al. 1993; Al Haidary et al. 2001). A more generalized effect of toxins on thermoregulation is found among laboratory rodents that exhibit a physiologically and behaviorally controlled reduction in body temperature (i.e., regulated hypothermia) when exposed to a variety of chemically diverse toxic compounds (Gordon et al. 1988). The fact that exposure to toxins under abnormal or artificial conditions influences thermoregulation suggests that toxins may play an integral role in the thermoregulatory physiology of herbivores that regularly ingest toxic plant secondary compounds.

The objective of our study was to investigate whether plant secondary compounds naturally occurring in the diets of mammalian herbivores influence thermoregulatory physiology in such a way as to influence the cost of thermoregulation. Specifically, we measured the effects of consuming one-seeded juniper (*Juniperus monosperma*) on three thermoregulatory parameters (body temperature, basal metabolic rate, and the

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minimum cost of thermogenesis) in the woodrats *Neotoma albigula* and *Neotoma stephensi* under conditions of warm and cold acclimation. Many of the secondary compounds in the one-seeded juniper (*J. monosperma*) are toxic (Adams et al. 1981). Alpha-pinene, the predominant monoterpene in juniper, can cause tissue damage and death in mammals (Sperling et al. 1967; Savolainen and Pfaffli 1978; Adams et al. 1981; Falk et al. 1990). The woodrats *N. albigula* and *N. stephensi* both include *J. monosperma* in their natural diet; *N. albigula* is a generalist that consumes 18%–35% juniper in its diet (Dial 1988), whereas *N. stephensi* is a juniper specialist (range in diet, 60%–80%, Dial 1988; 83%–96%, Vaughn 1982). The southwestern desert habitat of *N. albigula* and *N. stephensi* subjects them to high thermoregulatory stress and low resource availability during the winter. Therefore, any impact of dietary toxins on thermoregulatory ability and thermoregulatory cost is highly relevant to the ecology of woodrats and may demonstrate the thermoregulatory importance of plant secondary compounds among mammalian herbivores in general.

Material and Methods

Thermoregulatory Parameters

The three thermoregulatory parameters, body temperature (T_b), basal metabolic rate (BMR), and the minimum cost of thermogenesis (C_{\min}), reveal different information about the influence of toxins on thermoregulation. Changes in T_b can indicate a shift in the temperature set point of an animal. Also, changes in T_b have a direct effect on the cost of thermoregulation because the rate of heat loss to the environment is directly proportional to the difference between T_b and environmental temperature; even small changes in T_b can have a large effect on the cost of thermoregulation (Studier 1981). Changes in BMR indicate whether there are any changes in the animal's baseline rate of heat generation. The cost of thermogenesis (C) is a measure of metabolic rate relative to temperature gradient and describes the amount of metabolic energy required to compensate for thermal energy lost to the environment. C_{\min} describes the minimum amount of metabolic energy required to compensate for thermal energy lost to the environment, and changes in C_{\min} provide an indirect measure of changes in thermal conductivity. Minimum cost of thermogenesis is offered here as an alternative name for the same parameter commonly referred to as minimum conductance. Minimum conductance is a misnomer because true conductance is a function of surface area; true conductance for mammals can seldom, if ever, be measured because it is not feasible to accurately measure the surface area of thermoregulating mammals (McNab 1980). However, assuming the surface area of a given animal remains constant and assuming an animal is maintaining a constant T_b (i.e., heat loss = heat generated), any change in C_{\min} would indicate a change in conductance.

For mammals, metabolic rate typically follows a character-

istic temperature response curve. Across a specific range of ambient temperatures (T_{amb}), oxygen consumption does not change (i.e., the thermal neutral zone), but as T_{amb} drops below the lower critical temperature, oxygen consumption begins to increase (Fig. 1a; Schmidt-Nielsen 1993). The resting metabolic rate (RMR) of a mammal within its thermal zone would represent the BMR because that is where the metabolic rate is both minimal and independent of T_{amb} . The parameter C for any given T_{amb} is calculated according to the equation

$$C = \frac{\text{RMR}}{T_b - T_{\text{amb}}},$$

and C becomes minimal as T_{amb} drops below the lower critical temperature and RMR becomes directly dependent on T_{amb} . To calculate the BMR and C_{\min} of an animal, it is necessary to measure the RMR both at a temperature within the thermal neutral zone (for BMR) and at a temperature below the lower critical temperature (for C_{\min}). Preliminary trials were carried out in which the resting metabolic rates of *Neotoma albigula* and *Neotoma stephensi* were measured across a range of ambient temperatures. These trials revealed that both woodrat species conform to a typical mammalian response curve with reliably minimal rates of oxygen consumption occurring within a T_{amb} range of 30°–35°C (Fig. 1b). Further, C values plotted against T_{amb} for the same woodrats found that C reaches a reliably minimal value when T_{amb} is below 25°C (Fig. 1c). Therefore, all measurements of BMR for each woodrat were calculated from the RMR at 33°C, whereas all C_{\min} measurements were calculated from the RMR and body temperature at 15°C. Because the main objective was to assess changes in the total metabolic cost of thermoregulation in the woodrats, both BMR and C_{\min} in this study were measured as whole-animal rather than mass-specific values.

Animals Used

A total of eight adult *N. albigula* and nine adult *N. stephensi* were used. All animals were either trapped in Coconino County, Arizona, or were born in captivity to pregnant mothers collected from the same location. From the time of their capture or birth to the beginning of the experiment, all animals were maintained at 22°C at a 12L : 12D daily light cycle in the animal facility of the Biology Department, University of Utah. Each animal had been maintained in the animal facility on a diet of Harland Teklad rabbit chow 2031 for at least 6 mo before the start of the experiment.

Treatments

All animals were subjected to 13 wk at an ambient temperature of 25°C followed by 10 wk at an ambient temperature of 18°C. For both species of woodrat, a drop from 25°C to 18°C is a

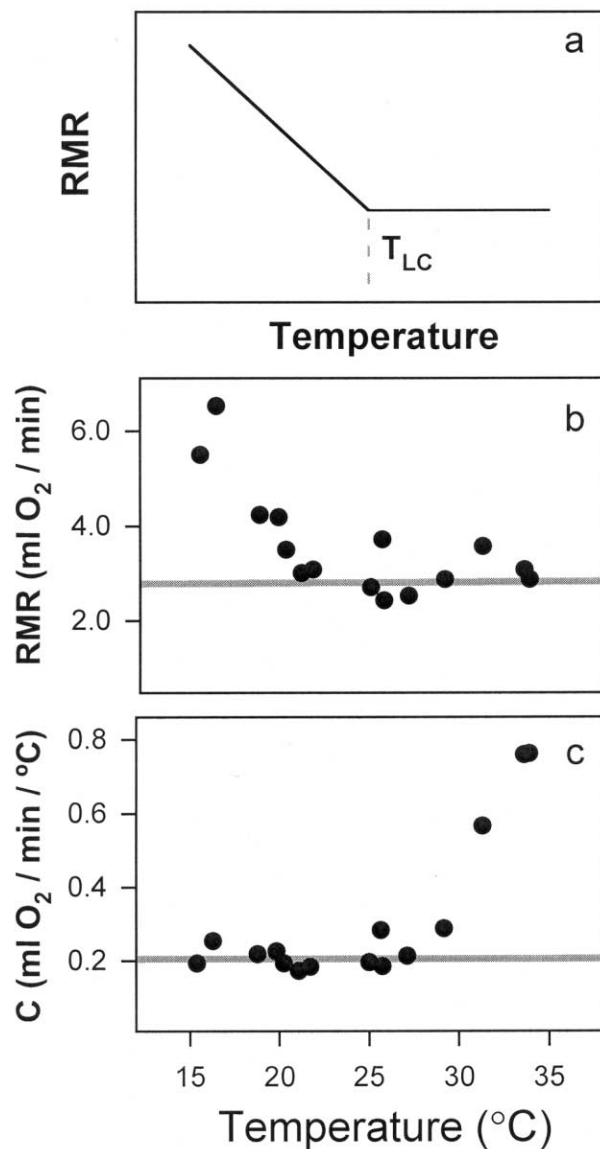


Figure 1. Idealized mammalian temperature response curve (a) plotting resting metabolic rate (RMR) as a function of ambient temperature across a range of ambient temperatures lower than the mammal's body temperature. In one distinct portion of the curve, the thermal neutral zone, RMR is independent of ambient temperature, whereas at temperatures below the lower critical temperature (T_{LC}), RMR is dependent on ambient temperature. Actual temperature response data for an individual woodrat *Neotoma albigula* (b) tend to follow the idealized pattern, reaching an apparent thermal neutral zone at ambient temperatures above 25°C. c, Plotting the cost of thermogenesis (C) against ambient temperature for the same individual shows that C reaches a stable minimum below temperatures of 25°C.

sufficient thermoregulatory stress to require a 50% or more increase in resting metabolic rates (Fig. 1b). When first exposed to each ambient temperature, each animal was given a 2-wk acclimation period during which they were fed Harland Teklad

rabbit chow 2031, followed by alternating periods of ad lib. control and ad lib. juniper diets. Each replicate diet treatment lasted 7–10 d, and under both acclimation temperatures, each woodrat was subjected to at least two replicates of control and two replicates of juniper diet treatments. The body mass of each animal was measured every 2–3 d. If animals lost more than 12% of their initial body mass, they were removed from the experiment. Animals were given free access to water during the entire course of the experiment.

The control diet consisted of ground rabbit chow, supplemented with cellulose, starch, sucrose, protein, oil, vitamins, and minerals, so as to be as dietarily similar to *Juniperus monosperma* as possible but without any of the secondary compounds (Dearing et al. 2000). The *J. monosperma* used for the diet was collected from the same field location as the woodrats and only from trees that showed signs of woodrat herbivory. To prevent excessive loss of any volatile secondary compounds in *J. monosperma*, the collected juniper was packed immediately on dry ice and kept frozen until use. The juniper diet was made by grinding the frozen juniper to a fine consistency and mixing it with an equal portion of control diet, forming a 50 : 50 mixture of juniper and control diet. Although 50% juniper is greater than generally observed by *N. albigula* in the field (Dial 1988), preliminary tests found that 50% juniper was the maximum level that *N. albigula* would eat to maintain themselves.

Under all treatment conditions, the animals were housed in 45 × 23 × 20-cm cages with wire mesh bottoms and running wheels. Each cage was furnished with a small square of cotton (10 × 10 cm) that allowed the animals to sleep comfortably but did not provide enough insulation to interfere with physiological temperature acclimation.

Measuring Metabolic Rates

During the last 2 d of each 7–10-d diet period, metabolic rates were measured. Each animal was placed inside a 500-mL metabolic chamber for 1 h. Temperature inside the metabolic chamber was maintained at either 15°C or 33°C by circulating either cold or warm water, respectively, through copper coils wrapped around the chambers. A temperature probe inside each chamber provided accurate measurement of T_{amb} . A constant airflow of 500 mL/min was drawn through the chamber. Each woodrat was allowed to get accustomed to the metabolic chamber for the first 30 min. During the second 30 min, the effluent airflow was channeled through an AEI oxygen analyzer after first passing through drying tubes containing Drierite and barium hydroxide to remove water vapor and CO₂, respectively. The oxygen analyzer calculated the fractional volume of oxygen in the effluent air to a precision of 0.01%, and LabVIEW software was used to calculate the total volume of oxygen consumed, adjusted to STPD, every 30 s. Calculation of oxygen consumption followed the procedure outlined by Depocas and Hart (1957) for an open-circuit system with the outlet air me-

Table 1: Effects of acclimation temperature (25°C vs. 18°C) and diet (control vs. juniper) for the woodrats *Neotoma albigula* and *Neotoma stephensi*

Species and Parameter	Treatment Combination (Acclimation Temperature/Diet)				Effects ^a
	25°C Control	25°C Juniper	18°C Control	18°C Juniper	
<i>N. albigula</i> (n = 8):					
Mass (g)	188.6 (±9.3)	169.4 (±9.7)	195.7 (±8.6)	177.7 (±8.0)	T**, D**
T _b (°C)	37.73 (±.17)	37.52 (±.16)	37.74 (±.22)	37.99 (±.19)	T**, I**
BMR (mL O ₂ /min)	2.65 (±.11)	2.57 (±.19)	3.83 (±.16)	3.58 (±.19)	T**
RMR _{15°C} (mL O ₂ /min)	4.68 (±.22)	5.60 (±.42)	6.63 (±.38)	5.83 (±.34)	T**, I**
C _{min} (mL O ₂ /min/°C)	.206 (±.010)	.248 (±.018)	.291 (±.015)	.253 (±.014)	T**, I**
<i>N. stephensi</i> (n = 9):					
Mass (g)	191.3 (±7.7)	195.0 (±6.6)	192.6 (±7.3)	198.5 (±6.5)	D**
T _b (°C)	37.61 (±.09)	37.77 (±.07)	37.66 (±.06)	37.80 (±.04)	D*
BMR (mL O ₂ /min)	2.30 (±.16)	2.26 (±.10)	2.94 (±.20)	2.89 (±.08)	T**
RMR _{15°C} (mL O ₂ /min)	4.98 (±.21)	5.83 (±.37)	5.49 (±.16)	5.66 (±.27)	D*
C _{min} (mL O ₂ /min/°C)	.220 (±.009)	.256 (±.016)	.242 (±.007)	.248 (±.012)	D*

Note. Effects on mean (±SE) body mass, body temperature (T_b), basal metabolic rate (BMR), resting metabolic rate at 15°C (RMR_{15°C}), and minimum cost of thermogenesis (C_{min}).

^a Indicates which treatment effects are significant (T = temperature acclimation, D = diet, I = T × D interaction); asterisks indicate the level of significance, determined by repeated-measures ANOVA.

* P < 0.05.

** P < 0.005.

tered. From each 30 min of oxygen consumption data recorded for each animal, the RMR was taken to be the average rate of oxygen consumption during the 6-min interval during which oxygen consumption was lowest.

Immediately after each hour inside the metabolic chamber, T_b was measured by inserting a probe 2–3 cm into the rectum. The temperature probe was a thermistor calibrated at 36°C and 40°C to generate a linear equation for converting the resistance of the thermistor into degrees Celsius. The thermistor resolved differences of 0.05°C. To minimize direct handling of the animals during T_b measurement, animals were transferred directly (and voluntarily) from the metabolic chamber to a short plastic tube that left their hindquarters exposed. The temperature probe was inserted for a duration of 45 s, and the woodrats were held secure in position in the tube by lightly pinching the base of the tail between thumb and forefinger.

Only one RMR measurement was taken for each animal per each day of each 2-d measurement period. To ensure that habituation effects did not confound the differences between values measured at 15°C and 33°C, one-half of the woodrats of each species had RMR measured at 15°C the first day and at 33°C the second day. The remaining woodrats had RMR measured at 33°C the first day and at 15°C the second day.

Statistical Analysis

The effects of diet (control vs. juniper), acclimation temperature (25°C vs. 18°C), and diet by acclimation interaction on T_b, BMR, and C_{min} for each species were tested statistically by

using repeated-measure ANOVAs. Many of the woodrats underwent a change in body mass during the course of the experiment, especially when switching from one diet to another. Changes in body mass can influence metabolic rates in a number of different ways. Therefore, to ensure that any observed effects of diet on T_b, BMR, and C_{min} could not be attributed to net weight loss or gain, any thermoregulatory parameter that exhibited a significant diet effect was subjected to an ANCOVA. For each woodrat, under warm- and cold-acclimation conditions, Δmass (i.e., the average body mass on juniper diet minus the average body mass on control diet) and the corresponding thermoregulatory parameters ΔT_b, ΔBMR, and ΔC_{min} were calculated. ANCOVA was then carried out on ΔT_b, ΔBMR, or ΔC_{min} using Δmass as the covariate.

Results

Thermoregulatory Parameters

Body mass, the values of the three thermoregulatory parameters, T_b, BMR, and C_{min}, and the RMR at 15°C (RMR_{15°C}) for both species under each treatment are shown in Table 1. In general, *Neotoma albigula* was more strongly affected by the treatments than *Neotoma stephensi*. In particular, temperature acclimation affected all the thermoregulatory parameters in *N. albigula* but only affected BMR in *N. stephensi*; interaction effects were more common in *N. albigula* as well. The fact that the data are reported in whole-body instead of mass-specific units had no bearing on the outcome of the analyses; repeating the analyses with mass-specific units yielded identical results.

Juniper consumption influenced T_b in both species, although the magnitude of the effects of juniper were very small (changes of 0.15–0.25°C). In *N. stephensi*, the effect of juniper consumption resulted in an increase in T_b regardless of acclimation temperature. However, in *N. albigula*, the effect of juniper consumption on T_b was dependent on acclimation temperature (i.e., no significant diet effect, but a significant interaction effect; Table 1) such that juniper caused T_b to decrease in warm-acclimated animals but increase in cold-acclimated animals. Acclimation temperature affected T_b in *N. albigula*, but this result may have been driven by the diet interaction effect because the T_b of warm- and cold-acclimated animals did not differ for animals on the control diet. A comparison of T_b values for individuals on control diet revealed that the average T_b of individual woodrats was highly correlated between the warm- and cold-acclimation conditions ($r = 0.86$; $P < 0.0001$). The ability to consistently resolve differences in T_b among individuals confirms the accuracy and reliability of the T_b measurements.

The only parameter to be affected similarly in *N. albigula* and *N. stephensi* was BMR. Acclimation to cold temperatures caused a significant increase in BMR of generally 30%–40% for both species, but there was neither a diet nor a temperature acclimation \times diet interaction effect in either species. The temperature acclimation effect is presumably due to the up-regulation of brown fat metabolism (Davis and Hillyard 1983) and demonstrates that the woodrats were given adequate time at 18°C for physiological acclimation to occur.

For *N. stephensi*, C_{\min} showed no significant effect of temperature acclimation and a significant effect of diet. For *N. albigula*, temperature acclimation caused significant changes in C_{\min} . Although there was no direct effect of diet on the C_{\min} of *N. albigula*, there was a highly significant temperature acclimation \times diet interaction in which juniper consumption resulted in elevated C_{\min} values when animals were warm-acclimated but reduced C_{\min} values when animals were cold-acclimated.

Mass Effects

Juniper diets resulted in significant changes in body mass for both species (Table 1), largely because *N. albigula* reduced their food intake when switching from control to juniper diets, whereas *N. stephensi* increased their food intake. Because diet had no effect on BMR, ANCOVAs were carried out on ΔT_b and ΔC_{\min} only. Furthermore, because *N. albigula* tended to lose weight on the juniper diet and *N. stephensi* tended to gain weight and because the effects of weight loss on thermoregulatory parameters may not necessarily be the same as the effects of weight gain, separate ANCOVAs were done on *N. albigula* and *N. stephensi*. Thus, a total of four ANCOVAs were carried out (two parameters \times two species). However, none of the ANCOVAs found Δ mass to be a significant covariate of the measured thermoregulatory parameters (P values for ΔT_b vs.

Δ mass were 0.63 and 0.08 for *N. albigula* and *N. stephensi*, respectively; P values for ΔC_{\min} vs. Δ mass were 0.31 and 0.98 for *N. albigula* and *N. stephensi*, respectively). Therefore, we conclude that the effects of juniper consumption on thermoregulation observed in this study were independent of any effects of juniper on body mass.

Juniper and the Cost of Thermoregulation

The general effects of juniper on the metabolic cost of thermoregulation can be seen by comparing values of $RMR_{15^\circ C}$ under each treatment (Table 1). In *N. albigula*, once again, the effect of juniper is dependent on acclimation temperature; juniper consumption tends to induce an increase in $RMR_{15^\circ C}$ among warm-acclimated *N. albigula* but tends to induce a decrease in $RMR_{15^\circ C}$ among cold-acclimated *N. albigula*. In *N. stephensi*, juniper consumption increases $RMR_{15^\circ C}$ independent of acclimation temperature (P value of the diet effect = 0.024; P value of diet \times acclimation temperature effect = 0.123), although the effect of juniper on $RMR_{15^\circ C}$ appears much more pronounced for warm-acclimated *N. stephensi*.

The relative effect of juniper on the cost of thermoregulation at 15°C can be measured by comparing the extent to which $RMR_{15^\circ C}$ is elevated above BMR for animals on juniper and control diet. For each animal at each acclimation temperature, the relative change in the cost of thermoregulation at 15°C caused by juniper consumption was calculated as a percent ratio of the difference between $RMR_{15^\circ C}$ and BMR on juniper diet (i.e., $[RMR_{15^\circ C} - BMR]_{\text{juniper}}$) and the difference between $RMR_{15^\circ C}$ and BMR on control diet (i.e., $[RMR_{15^\circ C} - BMR]_{\text{control}}$) using the following formula:

$$100\% \times \left[1 - \frac{(RMR_{15^\circ C} - BMR)_{\text{juniper}}}{(RMR_{15^\circ C} - BMR)_{\text{control}}} \right].$$

Because BMR did not differ in relation to diet for either species at either acclimation temperature, the BMR value used in the above equation was the average BMR of each individual on both diets.

The average relative changes in the cost of thermoregulation at 15°C caused by juniper consumption are shown for each species at each acclimation temperature in Figure 2. For both species, juniper consumption caused a significant increase in the relative cost of thermoregulation when animals were warm acclimated (50% and 33% for *N. albigula* and *N. stephensi*, respectively). However, the effect of juniper consumption on the cost of thermoregulation either disappears or becomes negative when the animals were cold acclimated. The average change in the cost of thermoregulation for cold-acclimated *N. stephensi* on juniper diet was an increase of 9%, but this value was not significantly greater than 0. Cold-acclimated *N. albigula* on juniper diet showed a 24% decrease in the cost of thermoregulation.

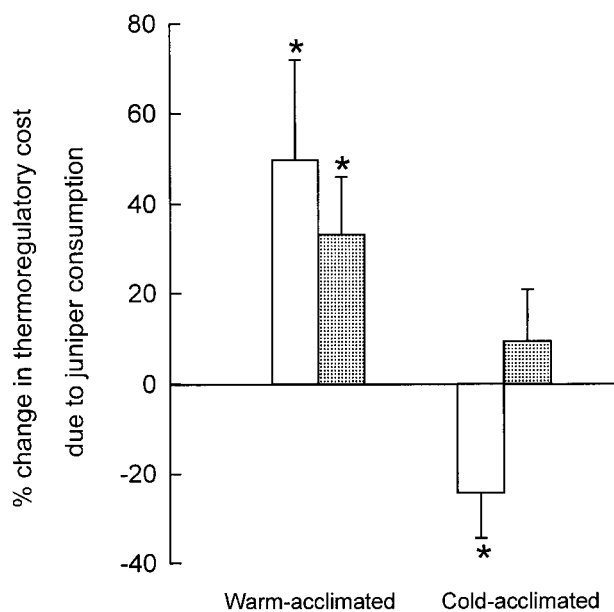


Figure 2. Average percent change in metabolic cost of thermoregulation at 15°C for the woodrats *Neotoma albigula* (open bars) and *Neotoma stephensi* (shaded bars) on juniper diet compared with control diet. Error bars represent standard error, and asterisks indicate means that are significantly different from 0 ($P < 0.05$).

The importance of considering the relative change in the cost of thermoregulation rather than just the absolute change is that it provides a basis for extrapolating the impact of juniper consumption on thermoregulation at temperatures lower than those used here. The absolute changes in $RMR_{15^{\circ}\text{C}}$ caused by juniper consumption measured in this study were not very large, but the low temperature used in this study was relatively mild compared with winter temperatures at the locality where the specimens of *N. albigula* and *N. stephensi* were collected (i.e., typically below freezing). Thus, although a 24% decrease in the cost of thermoregulation may not translate into a large amount of energy at 15°C, it could represent a substantial portion of the energy budget of *N. albigula* at 0°C.

Discussion

Juniper and Thermoregulation

The results of this study support the hypothesis that plant secondary compounds influence the cost of thermoregulation in mammalian herbivores. Something present in the juniper diet but absent from the control diet affects the thermoregulatory physiology of the woodrat *Neotoma albigula*. It is possible that an overlooked nutritional difference between the diets may be responsible because diets that differ in nutritional content can cause changes in metabolic activity (Rothwell and Stock 1987; Trier 1996). However, the nutritional compositions (i.e., amount of protein, carbohydrates, lipids, and fiber) were kept similar

between the control and juniper diets. Also, the lack of a diet effect on the BMR of either woodrat species suggests a nutritional similarity between the control and juniper diets. The most likely cause of the thermoregulatory effect of the juniper diet is one or more of the secondary compounds present in juniper.

The mechanism by which secondary plant compounds might induce the specific thermoregulatory responses observed in woodrats on a juniper diet is not clear. Given that T_b was observed to undergo only very small changes and, with the exception of warm-acclimated *N. albigula*, tended to increase for animals on a juniper diet, regulated hypothermia can be ruled out (Gordon et al. 1988). The effects of juniper consumption on C_{min} may be attributable to the presence of vasoconstricting or vasodilating agents present in *Juniperus monosperma* that alter peripheral blood flow, but the sensitivity of woodrats to these compounds would need to change in response to temperature acclimation to yield the observed results. Other juniper species contain a vasoactive compound (isocupressic acid; Gardner et al. 1998), and it is possible that *J. monosperma* contains the same substance. In addition to any effects on peripheral blood flow, juniper consumption may influence thermoregulation via changes in splanchnic circulation. If detoxification physiology leads to an increase in blood flow to the liver, the consequence would be a greater capacity to concentrate heat in the body core.

Similarities between the results of the warm-acclimated woodrats in this study and the results of a study by Bozinovic and Novoa (1997) suggest that some of the thermoregulatory effects of juniper may be due to tannic acids. Just as juniper consumption caused no change in BMR and an increase in $RMR_{15^{\circ}\text{C}}$ in warm-acclimated *Neotoma* spp., consumption of tannic acid caused no change in BMR and an increase in $RMR_{5^{\circ}\text{C}}$ in *Octodon degus* and *Phyllotis darwini* (Bozinovic and Novoa 1997). Furthermore, the percent relative increase in the cost of thermoregulation at 15°C for warm-acclimated woodrats on juniper diet was similar in magnitude to the percent relative increase in the cost of thermoregulation at 5°C for *O. degus* and *P. darwini* on a tannic acid-enriched diet (i.e., 30%–50%). Tannic acids are present in *J. monosperma* (Holechek et al. 1990). Thus, the thermoregulatory effects of juniper on warm-acclimated woodrats may be a common response of animals to the ingestion of tannic acid.

Another possible mechanism by which juniper consumption could influence thermoregulation in woodrats is via an effect on the microflora of the gut. The anaerobic fermentation reactions of symbiotic microorganisms can be a source of heat production that does not require elevated rates of oxygen consumption. Herbivores that rely on hindgut fermentation, such as woodrats, induce greater rates of fermentation under cold conditions by increasing dietary input (Yahav et al. 1993). If increased juniper consumption by cold-acclimated *N. albigula*, for example, causes an increase in the rate of hindgut fermentation and an elevation in anaerobic heat production, this could

lead to the observed decrease C_{\min} , because C_{\min} is a measure of the rate of aerobic heat production. However, the importance of hindgut fermentation as a heat source is not established, and it is also possible that the activity of the gut microflora of the woodrats acts as a heat sink rather than a heat source (Yahav and Buffenstein 1992).

Regardless of the underlying mechanism, the effect of juniper consumption on thermoregulation in *N. albigula* is ecologically interesting. In nature, *N. albigula* consumes more juniper during the winter than during the summer (Dial 1988). Previously, this pattern has been attributed to the lack of alternative food items during the winter (Dial 1988). However, if juniper consumption reduces the cost of thermoregulation in *N. albigula*, the possibility arises that *N. albigula* is deliberately seeking out juniper as a food source during the winter as a means of conserving energy. Furthermore, the eastern woodrat, *Neotoma floridana*, eats disproportionate amounts of red cedar (*Juniperus virginiana*) during the winter (Post 1991), suggesting that the selective foraging of particular plants could be a thermoregulatory strategy used by other species of woodrats and perhaps other mammalian herbivores as well.

Alternatively, the interaction effects between temperature acclimation and diet observed for *N. albigula* may reflect a coevolution between thermoregulatory and detoxification physiology. Because maximal thermoregulatory stress and maximal juniper exposure occur concurrently in *N. albigula* (i.e., they eat the most juniper when the temperature is the coldest), it is possible for the evolutionary response to both stresses to be physiologically linked in this species. No interaction effects were found between temperature acclimation and diet in *Neotoma stephensi*. However, there is no reason for thermoregulatory and detoxification to coevolve in *N. stephensi* because it eats high levels of juniper all year round.

Generalist versus Specialist

Generalizations concerning the differences between generalist and specialist herbivores based solely on the results of this study are subject to the same caveats as any two species comparison (Garland and Adolph 1994). However, *N. albigula* and *N. stephensi* are two closely related species exposed to the same environmental selection pressures that differ primarily in their dietary dependence of juniper. Therefore, it is reasonable to assume that differences in the physiological effects of juniper consumption between the two species are related in some degree to the difference in juniper specialization between them. Previous work has shown differences between *N. albigula* and *N. stephensi* in the degree to which they can tolerate a juniper diet and in the physiological pathways they use to detoxify juniper secondary compounds (Dearing et al. 2000; Sorensen and Dearing 2003). Differences in the thermoregulatory responses to juniper consumption by *N. stephensi* compared with *N. albigula* could be due to more effective elimination of juniper

secondary compounds or the specific evolution of a reduced sensitivity to the overall physiological effects of juniper.

Neotoma stephensi was also found to be more resistant to the effects of temperature acclimation than *N. albigula*. Every parameter presented in Table 1 was influenced by temperature acclimation in *N. albigula*, but only BMR was influenced by temperature acclimation in *N. stephensi*. Differences in the physiological dynamics of thermoregulation between *N. stephensi* and *N. albigula* are further demonstrated by the fact that, although both species are the same size, *N. stephensi* is able to maintain the same T_b as *N. albigula* even though it has a lower BMR than *N. albigula*. Therefore, differences in the effects of juniper on thermoregulation between *N. albigula* and *N. stephensi* may be due to differences in thermoregulatory physiology rather than differences in the physiology of juniper detoxification. It is not clear if anything links dietary specialization with reduced BMR and enhanced insulation, but the three traits have converged in other mammals in addition to *N. stephensi* (Degabriele and Dawson 1979; McNab 1984).

Cost of Detoxification

Earlier studies found an increased metabolic rate in mammals following the ingestion of plant secondary compounds (Thomas et al. 1988; Iason and Murray 1996) or following exposure to other dietary toxins (Voltura and French 2000). In this study, juniper had no significant effect on the BMR of woodrats in the absence of thermoregulatory stress. Woodrats do not exhibit long-term metabolic costs associated with the detoxification of juniper secondary compounds, and it is only under conditions of thermal stress when an effect of juniper on metabolic rates becomes apparent. Therefore, despite the lack of a direct metabolic cost of juniper detoxification, juniper can still influence total energy budgets via its influence on thermoregulatory physiology. The results of this study underscore the importance of considering the full physiological effects of plant secondary compounds when investigating the ecology and energetics of herbivores.

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