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Physiological limitations of dietary specialization in herbivorous woodrats (*Neotoma* spp.)

Jennifer S. Sorensen[a,*], M. Denise Dearing[b]

[a]*School of Pharmacy, University of Tasmania, Sandy Bay, TAS, 7005, Australia*
[b]*Department of Biology, University of Utah, USA*

Abstract. For nearly three decades, a fundamental objective in the study of plant–herbivore interactions has been to understand why the consumption of a single plant species is rare in mammals, as only a handful of mammalian herbivores (<1%) are dietary specialists. Here, we provide an overview of various factors that may play a role in limiting dietary specialization. We review the energetic consequences of ingesting PSMs and the physiological tradeoffs of specialization in a juniper specialist, *Neotoma stephensi*, and generalist, *N. albigula*, woodrat. In general, the energy budgets of specialist and generalist woodrats were negatively impacted by the intake of PSMs from juniper and novel PSMs. However, juniper specialists minimized the energetic costs associated with the intake of juniper through greater energy intake and lower energy expenditure than generalists and thus had more energy for other energy-dependent activities when consuming a juniper diet. Despite the high capacity to consume juniper, juniper specialists experienced a decreased ability to consume novel PSMs, suggesting a dietary trade-off associated with specialization. These data indicate that the energetic consequences of consuming PSMs and the dietary trade-offs associated with specialization may constrain dietary specialization in herbivorous woodrats. Identifying these factors and their role in limiting and/or facilitating dietary specialization in woodrats has provided a better understanding of the foraging ecology, physiology and evolution of mammalian herbivores in general. © 2004 Published by Elsevier B.V.

Keywords: Dietary specialization; Energy budget; *Neotoma*; Plant secondary metabolite; Trade-offs

1. Background

A fundamental objective in the study of plant–herbivore interactions has been to identify factors that limit dietary specialization in mammalian herbivores. The

* Corresponding author. Tel.: +61 3 6226 2232; fax: +61 3 6226 2870.
E-mail address: jennifer.sorensen@anu.edu.au (J.S. Sorensen).

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consumption of a single plant species is rare in mammals, as only a handful of mammalian herbivores (<1%) are dietary specialists [1]. One explanation for the paucity of mammalian specialists is that mammals are limited by the quality and quantity of secondary metabolites in plants [2–5]. It is theorized that dietary specialization in mammals is limited by the physiological challenges associated with the high quantities of a limited spectrum of secondary metabolites ingested in a diet of a single plant species. The few specialists that exist are predicted to have evolved mechanisms that overcome the physiological challenges of consuming a diet of a single plant species [5]. However, the mechanisms that facilitate dietary specialization may result in an evolutionary and/or ecological trade-off [6]. Specifically, specialists may be limited in the range of secondary metabolites they can ingest, thus restricting the habitats suitable for colonization by specialists. In the subsequent sections, we review the energetic consequences of ingesting plant secondary metabolites (PSMs), mechanisms that compensate for costs and physiological tradeoffs of specialization in a juniper specialist, *Neotoma stephensi*, and generalist, *N. albigula*, woodrat. These *Neotoma* species are an ideal pair of mammalian herbivores to synthesize the constraints of PSM ingestion because they are similar in body size, share habitats, have the same ecological and evolutionary experience with many PSMs (including those in juniper) and have been well studied with respect to their foraging behavior in the field and laboratory. Moreover, recent comparative work on these species demonstrated marked differences in their energetic and physiological capacities to handle various PSMs. Descriptions of these species, their diets, experimental approach, data analysis and results that are summarized here are found in detail in Sorensen et al. [7,8].

2. Energetic consequences of PSM intake

One major physiological challenge for mammalian herbivores is the energetic cost associated with the intake of PSMs. PSMs impinge on energy availability by diluting food energy [9,10], decreasing energy absorption [11–14], increasing the excretion of endogenous energy [15–19] and increasing energy expenditure [20–22]. The energetic consequences of processing both naturally consumed and novel PSMs are substantial in woodrats. In most cases, woodrats decreased intake (dry matter/day, Fig. 1) and, therefore, energy intake (Fig. 2) when consuming PSMs compared to diets without PSMs. In addition to reduced energy intake, woodrats also increased energy excretion (Fig. 2), resulting in decreased efficiency of energy metabolism. Energy lost in the urine alone represented up to 35% of basal metabolism in woodrats. This amount is on par with costs of reproduction and thermoregulation (10% and 37% of metabolism, respectively) in golden-mantled ground squirrels [23] and growth (36% metabolism) in cotton rats [24]. The intake of PSMs typically resulted in decreased apparent metabolizable energy (AMEI, kJ/day=ingested energy not excreted in urine and feces, Fig. 1).

Moreover, the energetic costs associated with the intake of PSMs can negatively impact energy available for critical activities (Figs. 1, 2). The intake of PSMs significantly compromised energy available for energy dependent activities and body mass. Woodrats consuming PSMs reduced the distance ran on running wheels and time spent running by up to 53% [7,8]. In most cases, the intake of PSMs also compromised

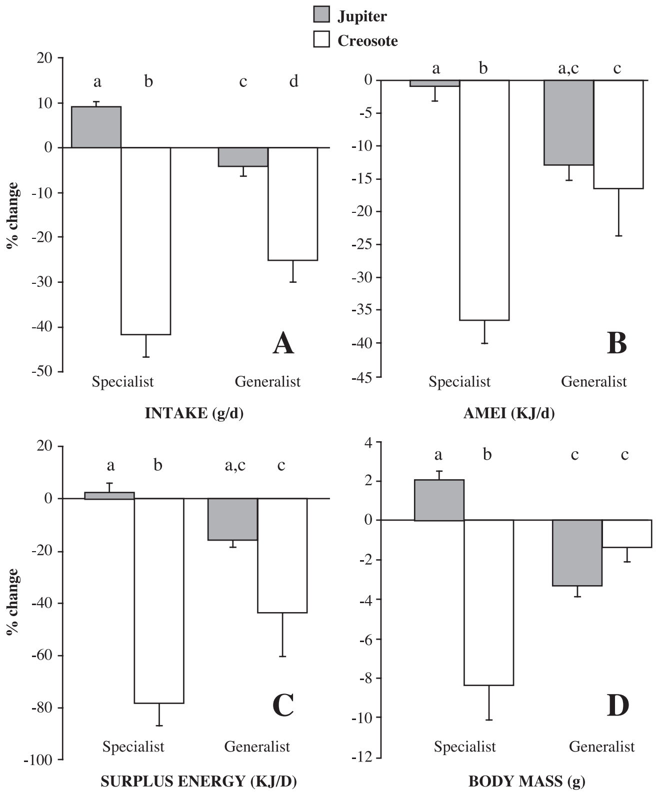

Fig. 1. Weekly percent change in (A) intake (g dry matter/day), (B) apparent metabolizable energy intake (AMEI, kJ/day=Energy intake (kJ/day)−exerted in feces (kJ/day) and urine (kJ/day)), (C) surplus energy (kJ/day=AMEI−energy spent on basal metabolic rate and voluntary wheel running) and (D) body mass for specialists and generalists on juniper and creosote diets compared to control diets. Different letters represent significant differences between means using Tukey's Honestly Significant Differences (hsd) procedure [41]. Bars are ± standard errors. Modified from Sorensen et al. [7,8].

surplus energy (i.e., ingested energy not lost in urine or feces or expended on metabolism or locomotion) needed for reproduction, thermoregulation, immunocompetency, etc. In addition, woodrats typically responded to reduced energy availability by catabolizing energy stores as indicated by loss in body mass when consuming PSMs (Fig. 1). These results highlight the substantial energetic consequence ingested PSMs can have on the overall energy budget and therefore fitness of mammalian herbivores.

3. Compensation for costs of ingested PSMs

Because energy is a limited resource, the few specialists that exist are predicted to evolve mechanisms that minimize the cost of processing PSMs and maximize energy availability. Consistent with this hypothesis, juniper specialists maintained higher surplus energy on juniper than generalists (Fig. 2). There are several factors that can contribute to maximizing surplus energy. Some specialist herbivores rely on inexpensive detoxification

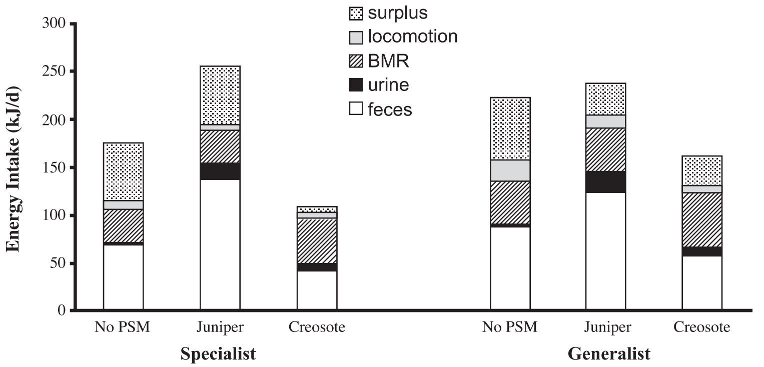

Fig. 2. Energy intake partitioned into energy exerted in feces and urine, expended on basal metabolic rate (BMR) and voluntary wheel running (locomotion) and surplus energy that could be available for reproduction, thermoregulation, immunocompetency, etc. Values are for specialists and generalists fed diets without PSMs and containing PSMs from juniper (*Juniperus monosperma*) or creosote (*Larrea tridentate*). Modified from Sorensen et al. [7,8].

pathways, such as oxidation, to a greater extent than expensive pathways, such as glucuronidation [25]. Glucuronidation results in the excretion of detoxification metabolites conjugated to glucuronic acid, a derivative of endogenous glucose. In woodrats, glucuronic acid comprised up to 12% of the urinary energy excreted on juniper diets, compared to 3% on control diets. Although both specialists and generalists increased glucuronic acid production on juniper diets, generalists excreted nearly twice the glucuronic acid per unit energy intake compared to specialists [7]. These data suggest that specialists rely on inexpensive detoxification pathways, whereas generalists utilize more expensive pathways such as glucuronidation. Although glucuronidation is one of many expensive detoxification pathways [26], reduced glucuronidation may be one physiological mechanisms that contributes to lowering the costs of processing toxins in specialists.

Increased food intake is an additional strategy that can maximize surplus energy [27–29]. However, for mammalian herbivores, greater intake of a single plant species also results in greater intake of PSMs. Compensatory feeding must therefore incorporate mechanisms that minimize the accumulation of PSMs in the body as intake of PSMs increase. Furthermore, it is predicted that dietary specialists should have adaptations for rapid elimination of PSMs and that these mechanisms will facilitate high levels of intake of PSMs from a single plant species [4,5]. In support, juniper specialists absorbed across the gut a lower proportion of ingested alpha-pinene, a predominant PSM in juniper, resulting in higher quantities of alpha-pinene excreted unchanged in the feces than generalists [30]. An enhanced capacity to eliminate ingested alpha-pinene is associated with lower blood levels of alpha-pinene per unit ingested and higher intake of juniper [31]. These data suggest that although compensatory feeding can maximize surplus energy, this strategy may be restricted to dietary specialists that possess mechanisms that effectively eliminate ingested PSMs.

Juniper specialists can further maximize energy availability by minimizing energy expenditure. Overall, specialists expended less energy on basal metabolic rate (BMR) and engaged in less locomotor activity than generalists, regardless of diet or PSM ingested

(Fig. 2, [7,8]). In addition, specialists tended to decrease BMR even further when consuming juniper diet. Data are consistent with the theory that specialization, particularly specialization on diets high in PSMs, favors reduced energy expenditure [32–34]. Data also support previous work that animals reduce metabolic rates and locomotion when costs of ingesting PSMs are high [33–36]. We propose that low BMR and PSM induced reductions in BMR in dietary specialists may be an energy compensation strategy to deal with the costs of PSM intake. Although reduced BMR and locomotor activity may compensate for energetic costs of PSM intake, there may be constraints on the ecological benefits of such a strategy. For example, low metabolism is often associated with reduced natal growth rates and fecundity in mammals [34]. Clearly, the fitness advantages and disadvantages of reduced expenditure associated with PSM intake and the role this plays in limiting dietary specialization deserve further investigation.

4. Dietary tradeoffs of specialization

Dietary tradeoffs of specialization may also limit the occurrence of mammals consuming a single species of plant. In general, specialization may be limited because specialists trade-off the ability to consume large quantities of a single plant for a reduced ability to consume novel plants [6]. The mechanisms responsible for reducing costs and enhancing excretion of secondary metabolites in the plants frequently consumed by specialists may be mechanistically and/or energetically less efficient at eliminating PSMs from novel plants. These predictions were tested by comparing the performance of juniper specialists fed juniper versus a novel plant, creosote, relative to the performance of generalists on the same diets. The phenolic resin from creosote bush (*Larrea tridentata*) contained PSMs that are novel to both specialists and generalists. Although the complete chemical profile of juniper, creosote and other plants consumed by specialists and generalists is unknown, there is strong evidence that specialists and generalists have not had evolutionary or ecological experience with the major PSMs in creosote [37–40].

The prediction that physiological trade-offs are associated with specialization was supported by studies on herbivorous woodrats. Juniper specialists were more energetically impacted by the intake of PSMs in creosote, a novel plant species, than juniper and were impacted to a greater extent than generalists (Figs. 1, 2, [8]). Juniper specialists reduced intake by 42%, AMEI by 36%, surplus energy by 79% and body mass by 8% when consuming creosote PSMs compared to diets lacking PSMs. In contrast, these parameter were not affected and often increased when specialists consumed juniper. In addition, creosote negatively impacted intake, AMEI, surplus energy and mass to a greater extent in specialists than generalists. Although generalists did reduce intake on creosote and did so to a greater degree than on juniper, reductions in AMEI, surplus energy and body mass were similar on both juniper and creosote diets. These data suggest that two distinctly different plants, one naturally consumed, one novel, each with different PSM profiles, have a similar negative effect on the performance of generalists. Data also suggest a dietary trade-off of specialization in mammalian herbivores in that juniper specialists trade-off their ability to perform well on juniper for a reduced ability to consume PSMs from a novel plant. A lower capacity to handle a wide range of plants may restrict specialization to a limited number of habitats where their preferred plant species is abundant. Furthermore, if specialists lack the capacity to exploit novel plant species they may be selected against if plant availability fluctuates.

5. Conclusion

Identifying the factors that limit and/or facilitate dietary specialization is essential to understanding the foraging ecology, distribution, physiology and evolution of mammalian herbivores. This review suggests that the energetic costs associated with consuming high quantities of a single plant species are significant and can negatively impact energy budgets. To overcome this energetic insult, mammalian herbivores may require physiological and behavioral mechanisms that mitigate the costs of processing PSMs or minimize energy expenditure. Specialization may therefore be limited by not only the costs of consuming high levels of PSMs, but also the capacity to eliminate PSMs and the consequences of reduced expenditure. In addition, once mammalian herbivores evolve to minimize costs of consuming a single plant species, they may face a dietary "dead-end", in that they have a reduced ability to consume novel species of plants. A limited ability to consume a variety of plants may make specialists less resilient to changes in their wild plant availability and restrict distributions to specific habitats. Although conclusions drawn here are restricted to a single pair of specialist and generalist mammalian herbivores and a single novel plant, this review provides a detailed overview of important factors that may limit dietary specialization in herbivorous woodrats. These data provide initial evidence that PSMs influence more than just the foraging behavior of mammalian herbivores and may also play a significant role in the physiology and evolutionary success of mammalian herbivores. However, it is essential to further test the impact of PSMs on energy budgets and the physiological tradeoffs of specialization using additional herbivores and species of plants to apply these findings to the specialists–generalist paradigm in general.

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