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Interacting effects of ambient temperature and food quality on the foraging ecology of small mammalian herbivores

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ABSTRACT

Both temperature and diet quality play an important role in the time and energy budgets of small mammalian herbivores. However, little is known about how temperature and diet quality interact to influence diet selection, nutrient extraction, and energetics, and how these effects might differ among species. Therefore, we examined the effects of diet quality and temperature on aspects of the foraging ecology of two species of lagomorphs, pygmy rabbits (*Brachylagus idahoensis*), which are small dietary specialists, and mountain cottontail rabbits (*Sylvilagus nuttallii*), which are larger dietary and habitat generalists. In a series of feeding experiments, we investigated 1) the effects of temperature on selection of plant fiber and the plant secondary metabolite 1,8 cineole in their diets, 2) effects of temperature and plant fiber on daily intake, digestion, and passage of food, 3) effects of plant fiber and 1,8 cineole on resting metabolic rate, and 4) how these interactions differ between the rabbit species. Both species chose to eat more total food and a greater proportion of high fiber food that passed more quickly through the digestive system in colder temperatures. However, temperature did not affect how much 1,8 cineole the rabbits consumed nor how thoroughly they digested food. Food quality affected how well they digested the dry matter in the food, but not their resting metabolic rate. Understanding how the interactions between ambient temperature and food quality affect selection of diets and intake by small mammalian herbivores, and the physiological mechanisms governing these choices, is useful for predicting how these species might respond to changes in both temperature and food quality and inform conservation and restoration strategies.

1. Introduction

To survive and reproduce in variable environments, small mammalian herbivores must adapt strategies to efficiently ingest and allocate energy. Their success depends on both the intrinsic properties of their food, such as concentrations of plant fiber and plant secondary metabolites, and on properties of the environment, such as food availability, the risk of predation, and thermal conditions. Consuming fibrous and chemically-defended food can reduce the rate and extent of digesting and metabolizing energy (Demment and Van Soest, 1985a, 1985b; Sorensen et al., 2005b). Likewise, foraging in temperatures outside of its thermal neutral zone (TNZ) increases a homeotherm's energy expenditure (Porter et al., 1994) or requires the animal to spend additional time using behavioral methods to buffer against these effects (Caraco et al., 1990). Furthermore, changing temperatures, both seasonal and long-term climatic trends, can influence the nutritional quality of forage plants available to herbivores, such as concentrations

of nitrogen, fiber and chemical defenses (i.e., plant secondary metabolites, Gershenson, 1984; Chapin et al., 1995; Jensen et al., 2016). Although the influence of dietary quality on foraging by herbivores has been well-studied, few studies have directly explored how interactions between environmental temperature and food quality affect the foraging ecology of small mammalian herbivores.

When possible, herbivores can increase their net energy gain by selecting food that is low in fiber and plant secondary metabolites and by foraging at sites or times when the temperature they experience is within their TNZ (Huey, 1991; Aublet et al., 2009; Orrock and Danielson, 2009). For example, alpine ibex (*Capra ibex*) in Italy, which have a low tolerance for heat, fed most actively during the coolest time of day and moved to higher elevations and spent less time feeding as the temperature and solar radiation increased (Aublet et al., 2009). Similarly, white-footed mice (*Peromyscus leucopus*) spent more time foraging on nights when the soil temperature was higher, presumably reducing their thermoregulatory costs (Orrock and Danielson, 2009).

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However, when ambient temperature or habitat conditions force herbivores to feed in patches below or above their TNZ, they might attempt to consume foods that generate or dissipate heat. Consuming higher fiber diets when temperatures are colder might allow animals to offset heat loss with endogenous heat generated through microbial fermentation of plant fiber (Noblet et al., 1985; Young, 1981; NRC, 1981; West, 1997). That said, the role of dietary fiber in thermoregulation, especially in small mammals, is unclear (Mader et al., 2001). In addition, ingesting some types of plant secondary metabolites might help endotherms maintain body temperatures within their TNZs by reducing heat dissipation through vasoconstriction or by producing heat during detoxification (Forbey et al., 2009). However, because ingesting fiber and plant secondary metabolites can cause animals to reduce their food intake, they might not be able to consume high enough levels of either to reduce thermoregulatory costs in cold temperatures (Dearing et al., 2000; Demment and Van Soest, 1985a, 1985b; Shipley et al., 2012; Sorensen et al., 2005a).

Another strategy herbivores might use when forced to feed in patches below their TNZ is to increase their intake of digestible energy to meet the increase in energetic demands of thermoregulation. Animals can do this by eating more total food, choosing higher quality foods (i.e., forage with higher digestible energy), or digesting food more thoroughly. However, cold temperatures often occur during winter when forage plants senesce and become more fibrous, thus less digestible. Herbivores can obtain energy from plant fiber through microbial fermentation, but this process is relatively slow and inefficient, especially in small, hindgut-fermenting herbivores (Demment and Van Soest, 1985a, 1985b). However, small herbivores have mechanisms that help them cope with lower quality diets. For example, small mammals can adjust to elevated energy demands in cold temperatures by increasing retention time of fibrous food in the digestive tract over a period of days, thereby increasing microbial fermentation and the digestion and absorption of nutrients (Felicetti et al., 2000; García et al., 1999; Gross et al., 1985; Hammond and Wunder, 1991; Jørgensen et al., 1996).

Because these complex functional relationships are not fully understood, we studied how temperature and food quality interact to shape diet selection, food intake and digestion, and energetics. We compared responses to diet quality and temperature of two species of lagomorphs, pygmy rabbits (*Brachylagus idahoensis*) and mountain cottontails (*Sylvilagus nuttallii*), that differ in life history characteristics, but co-occur in the semi-arid sagebrush (*Artemisia* spp.) steppe in the intermountain west of the United States. Animals inhabiting these landscapes are exposed to extreme seasonal temperature variation from as low as -40°C during winter and as high as 45°C during summer (Knapp, 1997). Pygmy rabbits are habitat and dietary obligates (Green and Flinders, 1980), thus are restricted to sagebrush steppe, whereas generalist mountain cottontails use a wide variety of foods and habitats, and neither rabbit species has adapted hibernation to cope with temperature extremes and seasonal changes in food quality.

Because they differ in body size and tolerance for plant secondary metabolites, pygmy rabbits and cottontails would be expected to respond differently to food quality in relation to ambient temperature. Pygmy rabbits (~ 450 g) are less than half the size of cottontails (~ 1100 g), with higher mass-specific energy requirements, lower ability to digest fiber (Shipley et al., 2006), and potentially a narrower TNZ and greater tolerance to heat (McNab, 2002). Although the TNZ for mountain cottontails has not been documented, the lower critical temperature for winter-acclimatized pygmy rabbits is between 15°C and 18°C and the upper critical temperature is predicted to be between 23°C and 28°C (Katzner et al., 1997). In addition, pygmy rabbits, unlike cottontails, have special adaptations for efficiently detoxifying and eliminating the high levels of monoterpenes in sagebrush, their primary food source (Shipley et al., 2012).

To examine the interactions between temperature and food quality, we conducted a series of feeding experiments with captive pygmy

rabbits and cottontails. We first investigated the effects of temperature on selection of plant fiber and plant secondary metabolites (i.e., monoterpenes) in their diets. Next, we measured the effects of temperature on daily intake, digestion, and passage of food in relation to fiber content. Finally, we examined the effects of plant fiber and plant secondary metabolites on resting metabolic rates. We predicted that both rabbit species would choose to consume diets higher in fiber and monoterpene concentration in relatively colder temperatures to help generate heat for thermoregulation, but that the pygmy rabbits would increase their consumption of fiber to a lesser degree, and their consumption of monoterpenes to a greater degree, than would cottontails. To compensate for the increased energy cost of thermoregulation, we predicted that both species of rabbits would either consume more food or digest it more thoroughly in cold temperatures relative to warm temperatures. Forage digestibility in herbivores depends on time exposed to microbial fermentation (Cork, 1994); therefore, we expected the passage rate of food to increase with an increase in intake and a decrease in temperature. Because consuming higher fiber requires additional mechanical and chemical processing of food (Cork, 1994) and consuming monoterpenes requires using energetically expensive detoxification pathways (Sorensen et al., 2005b), we predicted that by consuming lower quality diets, both rabbit species would respond with an increase in resting metabolic rate.

2. Methods

2.1. Capture and maintenance of study animals

We captured pygmy rabbits for these experiments in Camas and Lemhi Counties in Idaho and Beaverhead County in Montana, USA (Idaho Wildlife Collection Permits #010813 and 100310 and Montana Scientific Collection Permit #2014-062), at elevations ranging from 1463m to 1819m. We captured mountain cottontail rabbits in Whitman County, Washington (Washington Scientific Collection Permit #13-102, Washington State University Institutional Animal Care and Use Committee Protocol #4398), at an elevation of 717 m. Capture weights for pygmy rabbits ranged from 350g to 500 g and 1080–1120 g for cottontails. Animals had lived in captivity at the Small Mammal Research Facility at Washington State University, Pullman, Washington, USA, for at least a year before experiments commenced. While they were not participating in experiments, rabbits were housed individually on pine shavings in $1.2\text{ m} \times 1.8\text{ m}$ enclosures. We fed the rabbits ad libitum a basal diet of water, completely-balanced commercial rabbit pellets (Purina Professional Rabbit Chow, Purina Mills, LLC, St. Louis, MO, 36% Neutral Detergent Fiber, NDF), greenhouse-grown forbs, and wild-grown sagebrush. Rabbits were provided with a nest box and a 3-m long, 4-cm diameter tube or a wooden hutch for security cover.

2.2. Assessing the effects of temperature on selection of food with plant fiber and plant secondary metabolites

To determine if rabbits would respond to lower temperatures by voluntarily consuming diets higher in plant fiber or plant secondary metabolites, we conducted a series of feeding trials with 6 pygmy rabbits (453 g, SD = 43 g) and 6 cottontails (1137 g, SD = 73 g) housed at 3 temperatures. These experiments took place during the winter, between 05 December 2015 and 22 January 2016. Rabbits were housed in $50\text{ cm} \times 50\text{ cm} \times 40\text{ cm}$ stainless steel crates in temperature controlled greenhouses at either 10.0°C (below lower critical temperature for winter acclimatized pygmy rabbits), 18.3°C (within TNZ), or 26.7°C (above TNZ; Katzner et al., 1997), which reflect temperatures in the animals' natural habitat. For the trials with plant fiber, we created diets of high fiber (50% NDF) by adding rice hulls (77% NDF) to the basal diet using a pellet mill (PM605, Buskirk Engineering, Ossian, IN, USA). Both rabbit species were offered a choice between the basal

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