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Comparisons and Contrasts between the Foraging Behaviors of Two White-tailed Ptarmigan (*Lagopus leucurus*) Populations, Rocky Mountains, Colorado, and Sierra Nevada, California, U.S.A.

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Abstract

The summer diets of a natural population of white-tailed ptarmigan (*Lagopus leucurus*), an herbivorous alpine grouse, in the Rocky Mountains and an introduced population in the Sierra Nevada were compared to determine if differences in alpine tundra plant communities affected nutritional intake. Foraging selections of 28 adult ptarmigan were recorded regarding number, amount, availability, nutritional, mineral and energy content of plant species eaten. The average diet of the Rocky Mountain ptarmigan was composed of nine plant species (99% g dry wt), while the average diet of the Sierra Nevada ptarmigan was composed of only two plant species, *Salix anglorum* and *Carex jonesii* (99% g dry wt). Although plant species eaten differed between the populations, the energy and lipid content of the diets were nearly identical. The diet of Sierra Nevada ptarmigan was 28% higher in protein and 13% lower in carbohydrate than the diet of Rocky Mountain ptarmigan, likely due to high consumption of *Salix* leaves and low consumption of flowers by the Sierra Nevada ptarmigan. Both populations exhibited sampling behavior (ingesting occasional bites from many species), which would allow ptarmigan to track changing resources in the highly variable alpine environment and may have enabled the introduced ptarmigan to identify a suitable diet.

Introduction

Alpine habitats are characterized by extremes in environmental conditions; consequently, alpine herbivores encounter widely differing food resources, both seasonally and locally. However, an animal's physiological requirements may not be as variable as its food resources. Energy requirements and macronutrient proportions are typically specific depending on the species of bird and age class (Robbins, 1983; Perry, 1984). Furthermore, because one plant species rarely, if ever, provides the full complement of a vertebrate herbivore's nutritional needs, a mixture of foods is required (Freeland and Janzen, 1974; Westoby, 1974; Pulliam, 1975; Belovsky, 1978, 1990; Milton, 1979; Batzli et al., 1980; Oates et al., 1980; Crawley, 1983). Foraging plasticity may be particularly essential for alpine herbivores to identify optimal mixtures of food species to meet their nutritional demands. Behavioral plasticity is defined as an array of immediate, reversible adaptive responses to environmental conditions (Klopfer and MacArthur, 1960; Morse, 1980; West-Eberhard, 1989) and an increase is predicted in animals' foraging plasticity in areas of high environmental variability, such as the alpine (Komers, 1997). In this study, we compared the diets of two populations of white-tailed ptarmigan (*Lagopus leucurus*), a North American alpine grouse that is herbivorous, to determine if and how the diets differed between widely separated mountain ranges with differing plant communities regarding plant species eaten and nutritional content of the diets. One population was located in the Front Range of the Rocky Mountains, Colorado, which is within the natural range of white-tailed ptarmigan. The other population was located in central Sierra Nevada, California, which is a range historically uninhabited by white-tailed ptarmigan (Clarke and Johnson, 1990) until this species was introduced in 1971–1972 from populations in the Rocky Mountains. The alpine plant community of the Sierra Nevada presented a unique array of forage species to the introduced ptarmigan. Numerous cosmopolitan alpine species, and species present in other North American alpine communities, are absent in the Sierra Nevada (Smiley, 1921; Sharsmith, 1940; Chabot and Billings, 1972; Billings, 1974, 1978). The lack of various alpine plant species may be due to factors including the relative youth of this range, climate, soil types, geological factors, and/or isolation from sources of colonists. We investigated the hypotheses that, due differences in alpine tundra plant community composition, white-tailed ptarmigan in the Sierra Nevada differed from the parent population in the Rocky Mountains regarding (1) plant species eaten, (2) foraging strategies, and (3) energy and nutritional intake.

Methods

The Rocky Mountain study area, along Trail Ridge Road, Rocky Mountain National Park, Larimer County, Colorado (40°26′N, 105°45′W), included 5.13 km^2 and ranged in elevation from 3800 to 4010 m. The Sierra Nevada study area, in the Hall Natural Area, Inyo National Forest, Mono County, California (37°58′N, 119°18′W), encompassed 7 km^2 ranging in elevation from 3050 to 3660 m. Foraging behaviors of 28 adult (≥2 yr old) female and male white-tailed ptarmigan were observed and recorded: 10 in the Rocky Mountains (4 females, 6 males) and 18 in the Sierra Nevada (8 females, 10 males). Data were collected for 4 wk in July 1986 and 1987 in the Rocky Mountains, and 6 wk in July 1985–1987 in the Sierra Nevada, during the peak of flowering in both locations. Each bird was banded with a unique combination of color bands and a numbered USFWS metal band.

Foraging observations of each bird were made in three periods, each on a different day: early morning, mid-day, and late afternoon. A minimum of three "foraging bouts" (eating for 5–20 consecutive minutes without leaving a foraging patch) were obtained for each bird. The array of foods eaten during a bout was a meal and an "individual's diet" was determined using number of bites and bite weight measures

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TABLE 1

Nutrient content of the nine plant species that were major contributors to >99% (g dry wt) of the summer diets of adult white-tailed ptarmigan in the Rocky Mountains, Colorado. Nine other species were sampled by the ptarmigan in amounts contributing <1% to the diets: Anemone narcissiflora, Artemisia pattersonii, Cerastium berringianum, Draba crassifolia, Juncus drummondii, Lloydia serotina, Saxifraga cernua, Sibbaldia procumbens, *and moss species.*

	Diet	Pro	CHO	Lipid	Ash	K	Ca	P	Mg	Na	Fe	Zn	Mn	Cu
	(%)	Mg g^{-1}								μg g^{-1}				
Acomastylis rossii	39.86	150	170	47	60	18	3.8	4.1	3.5	100	63	31	40	10
Bistorta vivipara	15.80	210	150	20	48	14	2.1	3.6	2.4	100	43	50	100	10
Dryas octopetala	12.51	150	260	37	45	15	2.9	3.0	1.8	200	52	40	87	10
Bistorta bistortoides	7.26	220	250	32	75	20	5.5	4.6	4.0	100	86	71	160	8
Trifolium dasyphyllum	6.60	310	190	35	73	12	12.0	4.2	2.5	100	52	40	87	10
Ranunculus adoneus	5.22	260	170	40	82	25	15.0	6.2	2.7	500	179	52	48	27
Lidia obtusiloba	4.55	150	240	20	67	14	3.0	2.8	1.7	400	609	44	71	7
Trifolium nanum	4.38	220	340	17	69	16	7.4	3.3	2.0	100	52	42	43	8
Salix reticulata	3.16	220	250	28	51	14	4.1	3.9	3.5	500	34	88	76	10
Total	99.34													

for >3 meals per bird. Bites per plant species per bout were recorded using abbreviations and tick marks on a ruled sheet without the observer taking his or her eyes off the foraging bird. Bite weight of each plant species was determined by selecting recently browsed parts (leaves, flowers, seeds) from forage plants, measuring bite size taken, and meticulously snipping out equally sized bites from intact portions of the plant (with manicure scissors). An average bite weight was determined using 10 such reproduced bites from each species. Bite weight was multiplied by number of bites to calculate relative contribution of each plant species to each bird's diet.

A "foraging patch" was the 1-m^2 area around a ptarmigan at the onset of a foraging bout. To obtain an "availability index" for each plant species, cover measures for each plant species in each foraging patch were obtained using a 1-m^2 plot with cross-hairs that divided it into four nested quadrats (Braun-Blanquet, 1932) and these measures were converted to percent gram dry weight cover by weighing samples of clipped plants. The use of weight measures for ptarmigans' bites and weight measures for plants' availability indices allowed for direct comparisons. Plant species' availability indices in 1-m^2 random patches (one for each foraging patch) were also measured and summed to form an index of plant availability in random areas. Henceforth, "availability index" will be referred to as simply "availability." We identified plants using the flora by Weber and Wittmann (1992) and Weeden (1981) with one exception. In the Rocky Mountain study site, alpine willows in the genus *Salix* are believed to hybridize (Martinsen et al., 2001); thus, we refer to all willow eaten as *Salix* spp., although *S. reticulata* appeared to be the primary dwarf alpine willow species consumed.

Feeding preferences may be determined by comparing the proportions of each item in the diet to its relative availability (Ivelv, 1961). These two variables will differ significantly if strong selectivity for or against particular foods is occurring (Chesson, 1978; Bryant and Kuropat, 1980; Kitting, 1980). Using SAS (SAS Institute, Inc., 1988), nonparametric statistics were employed in these analyses because of non-normal distributions (Shapiro-Wilks test, $P < 0.05$; Siegel and Castellan, 1988). For each population, Spearman rank correlations were used to determine if and how plant species' proportions in diets were related to the species' proportional availabilities in foraging areas. For each population, Mann-Whitney U tests were used to determine if the proportion of each food in each bird's diet differed from the food's relative availability in each bird's foraging area. Selection for or against a food was indicated when the relative amounts of a food in the diet differed significantly from that food species' relative availability in foraging areas. Random foraging was indicated when the relative amounts of a food in the diet matched that food species' relative availability in foraging areas. For each population, Mann-Whitney U tests were used to determine if plant species' availabilities in foraging areas differed from random areas. Significance levels of $P \leq 0.05$ were used. Samples of specific parts eaten from each forage species were collected for nutritional analyses. Wet weights were obtained in the field and then samples were placed in a plant press, oven dried later at 90°C for 12 h and reweighed to determine water content. Dried samples of each forage species that contributed ≥0.03% gram dry weight to the diets were analyzed by Weld Laboratories, Greeley, Colorado, for protein (Kjeldahl, using the conversion of 6.25 × N), total carbohydrate (ADF and by difference), and lipid (diethyl ether extract). Other nutrients and minerals (K, Ca, P, Mg, Na, Fe, Mn, Zn, and Cu) were analyzed courtesy of M. K. Meilahn, University of Northern Colorado, Greeley. An index of dietary energy (kJ g^{-1}) content was calculated using the classical Atwater energy conversion factors: 16.74 kJ g^{-1} protein, 16.74 kJ g^{-1} carbohydrate, and 36.65 kJ g^{-1} lipid (Merrill and Watt, 1955; Patrick and Schaible, 1980). Differences between the populations in nutrient and energy intake were examined using Mann-Whitney U tests. Significance was determined at $P < 0.05$. Nutrient, mineral, and energy content of the diets were calculated using major plant species contributing to 99% of diet weight. Data were pooled for each population because, within each population, birds did not vary significantly from one another in the numbers or amounts of plant species consumed nor did availabilities of the food species differ between the birds' foraging areas. Also, within each population, no differences in these variables existed between the sexes or the years.

Results

FORAGING SELECTIONS OF PTARMIGAN IN THE ROCKY MOUNTAINS

White-tailed ptarmigan observed in the Rocky Mountains consumed 18 plant species (Table 1). Nine of these species made up >99% of the average diet: *Acomastylis rossii* (alpine avens flowers), *Bistorta vivipara* (alpine bistort bulbils), *Dryas octopetala* (alpine dryad flowers), *B. bistortoides* (American bistort bulbils), *Trifolium dasyphyllum* (alpine clover flowers and leaves), *Ranunculus adoneus* (snow buttercup flowers and leaves), *Lidia obtusiloba* (alpine sandwort flowers), *T. nanum* (dwarf clover flowers and leaves), and *Salix* spp. (alpine willow species leaves). The other nine species in the diets were eaten rarely and in minute quantities, i.e. sampled, and together contributed <1% to the average diet.

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TABLE 2

Nutritional content of the two plant species that were major contributors to 99% (g dry wt) of the summer diets of adult white-tailed ptarmigan in the Sierra Nevada, California. Eleven species were sampled by the ptarmigan in amounts contributing <1% to the diets: Antennaria alpina, Arabis lemmonii, Cassiope mertensiana, Claytonia nevadensis, Draba lemmonii, Juncus drummondii, Lewisia pygmaea, Phyllodoce breweri, Ranunculus eschscholtzii, Sibbaldia procumbens, *and moss species.*

	Diet	Pro	CHO	Lipid	Ash	K	Ca	P	Mg	Na	Fe	Zn	Mn	Cu
	(%)	Mg g^{-1}								μg g^{-1}				
Salix anglorum	92.00	250	170	29	62	16	7.2	5.2	2.3	300	46	110	110	6
Carex jonesii	7.01	170	260	88	59	17	2.6	4.1	2.0	200	46	67	170	19
Total	99.01													

In foraging areas, the nine major contributors to the ptarmigans' diets were eaten in a seemingly random manner as evidenced by: (a) amounts consumed were positively correlated with availabilities and/or (b) relative percentages of these foods in the diets and these species' availabilities did not differ significantly. The three major foods in the diet (*A. rossii*, *B. vivipara*, and *D. octopetala*) were always eaten when present, but amounts eaten were positively correlated with availabilities ($r_s = 0.7939$, 0.8620, 0.9826, respectively; $P < 0.01$, all cases) and relative percentages of these foods in the diets and the availability of these foods did not differ significantly. Similarly, positive correlations existed between the amounts eaten and availabilities of *R. adoneus*, *L. obtusiloba*, *T. nanum*, and *Salix* spp. ($r_s = 0.7663$, 0.9416, 0.7462, 0.8824, respectively; $P < 0.05$, in all cases), and also relative amount eaten did not differ significantly from relative availability for any of these species. Although no correlation existed between amounts in the diet and availability for *B. bistortoides* or *T. dasyphyllum*, relative amounts in the diet did not differ from the relative availabilities of these two species.

No differences existed between foraging areas and random areas regarding food species' availabilities, with three exceptions. Foraging areas contained more *B. vivipara* ($z = -2.3642$, $P < 0.02$), *D. octopetala* ($z = -2.0710$, $P = 0.04$) and *B. bistortoides* ($z = -2.9119$, $P < 0.01$) than random areas. Hence, the birds appeared to be selecting specific foraging areas with high availability of these foods.

The remaining nine plant species eaten by the Rocky Mountain ptarmigan were sampled in quantities that contributed <1% (range = 0.01–0.30%) to the average diet. The amounts ingested did not differ significantly from these species availabilities with two exceptions: selection was exhibited against a sage and a mustard species. The sage, *Artemisia pattersonii* (Patterson's sage) was present in all foraging areas, but it was consumed rarely (three bites) and in amounts significantly less than the sage's availability ($z = -3.7935$, $P < 0.001$). The mustard, *Draba crassifolia*, was also eaten in amounts less than its availability ($z = -1.9216$, $P < 0.05$).

The major food in the diet, *A. rossii*, had the highest lipid content of any food eaten (Table 1). *Trifolium dasyphyllum* leaves had the highest level of protein, while the flowers of the other clover species eaten, *T. nanum*, had the highest carbohydrate content. *Ranunculus adoneus* flowers and leaves were highest in potassium, calcium, phosphorus, sodium, and copper. Magnesium was highest in *B. bistortoides* bulbils; *L. obtusiloba* flowers had high iron content, while sodium and zinc were high in *Salix* spp. leaves. The nutritional content of *A. pattersonii*, which was selected against, was notable only because it was high in manganese (280 μg g^{-1}). Water content in ingested plant material was 78% (based on weight) of the average diet eaten by white-tailed ptarmigan in the Rocky Mountains.

FORAGING SELECTIONS OF WHITE-TAILED PTARMIGAN IN THE SIERRA NEVADA

In the Sierra Nevada, ptarmigan were observed to consume 13 plant species, but two species made up >99% of the average diet (Table 2). The remaining 11 species were eaten in a manner indicative of "sampling" (eating occasional bites of a wide variety of foods). The leaves of *Salix anglorum*, dwarf willow, dominated every ptarmigans' diet in the Sierra Nevada. The relative amounts of *S. anglorum* in the diets exceeded its relative availability and the two measures were not correlated, indicating strong selection for this food. All foraging areas contained willow, and foraging areas contained more willow than did random areas ($z = -4.3313$, $P < 0.001$), indicating that the birds are selecting areas with high availability of this species. All ptarmigan observed in the Sierra Nevada ate the seed heads of the dwarf sedge *Carex jonesii*. Also, all foraging areas contained *C. jonesii*, and the availability of this sedge was greater in foraging areas compared to random areas ($z = -3.9351$, $P < 0.001$), again indicating selection for foraging areas containing this food.

As mentioned above, ptarmigan in the Sierra Nevada ingested 11 other species that contributed <1% (range = 0.01–0.32%) to the average diet. None were included in the diets in relative amounts exceeding their relative availability. *Phyllodoce brewerii* (red heather) and *Ranunculus eschscholtzii* (alpine buttercup) contributed 0.32 and 0.31% to the average diet weight, respectively, but, unlike *S. anglorum* and *C. jonesii*, they were not present in every foraging area. Ptarmigan ate the flowers of *P. brewerii* and *R. eschscholtzii* in amounts positively correlated with the availabilities of these species ($r_s = 0.4925$ and 1.000, respectively; $P < 0.05$, both cases) and availability of these species did not differ between foraging and random areas. Only one species, *Antennaria alpina*, was more available in random areas than in foraging areas ($z = 2.6471$, $P < 0.01$). No significant differences existed between availabilities in foraging and random areas for the other eight food species sampled.

The leaves of the willow, *S. anglorum*, contained levels of protein 47% higher than in *C. jonesii* (Table 2). Calcium, phosphorus, zinc, and manganese levels were also higher in *S. anglorum* than in *C. jonesii*. However, the lipid level of *C. jonesii* was more than twice the lipid level of *S. anglorum*, and carbohydrate content of the sedge seeds was 53% higher than in willow leaves. Regarding two foods that contributed ≥0.30% to the average diet, *P. breweri* was high in carbohydrate (260 mg g^{-1}) and sodium (500 μg g^{-1}), and *R. eschscholtzii* was high in protein (260 mg g^{-1}), sodium (500 μg g^{-1}), potassium (25 mg g^{-1}), phosphorus (6.3mg g^{-1}), and iron (175 μg g^{-1}). Water content in ingested plant material was 70% (based on wt) in the average diet of ptarmigan in the Sierra Nevada.

NUTRIENT, ENERGY, AND MINERAL COMPARISONS BETWEEN DIETS

Despite differences in plant species eaten, the estimated energy content of the Sierra Nevada birds' diets did not differ from the Rocky Mountain ptarmigans' diets ($\bar{X} = 8.20$ kJ g^{-1}, range = 7.64–8.75 kJ g^{-1}; $\bar{X} = 7.86$ kJ g^{-1}, range = 7.41–8.94 kJ g^{-1}, respectively; Fig. 1c). Compared to the diets of white-tailed ptarmigan in the Rocky Mountains, protein intake of the Sierra Nevada ptarmigan averaged 28.5% higher

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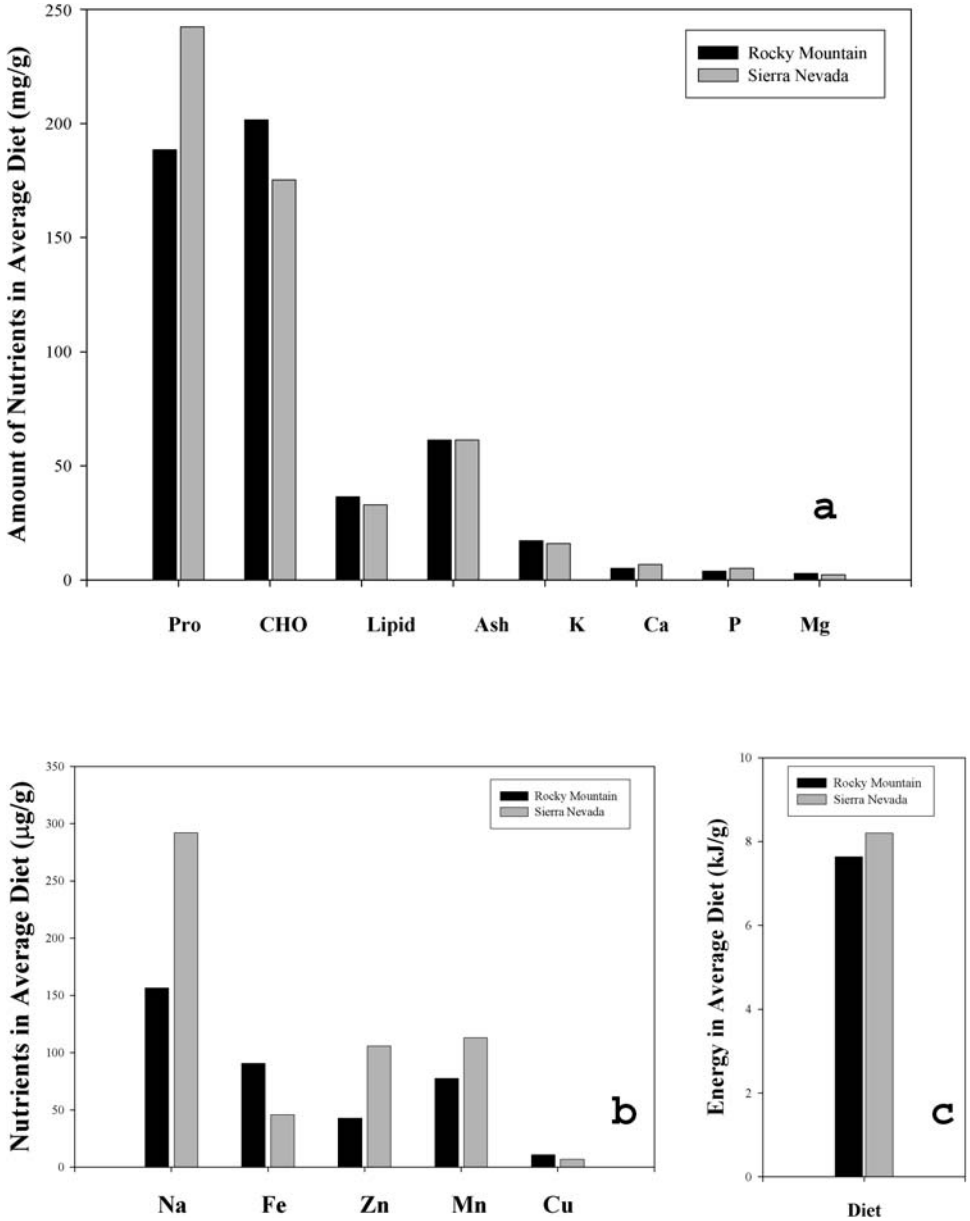

*FIGURE 1. Comparisons of (a) major nutrient content, (b) micronutrient content, and (c) total energy content of the average diets of white-tailed ptarmigan in the Rocky Mountains (*N = *10 adult birds) and the Sierra Nevada (*N = *18 adult birds).*

($z = -4.2917$, $P < 0.001$; Fig. 1a), while carbohydrate intake averaged 13% lower ($z = 3.1409$, $P < 0.02$) and lipid content did not differ significantly between the two populations' diets (Fig. 1a, $P > 0.05$). The major contributor to the high protein levels in the diets of the Sierra Nevada ptarmigan was *S. anglorum* (protein level: 260 mg g^{-1}). Ash content of the populations' diets did not differ significantly. Potassium content did not differ between the diets but Rocky Mountain ptarmigans' diets were lower than the Sierra Nevada birds' diets in calcium and phosphorus ($z = -3.1985, -4.1011$, respectively; $P < 0.01$, both cases), as well as sodium, zinc, and manganese ($z = -3.4286, -4.2923, -3.5250$, respectively; $P < 0.01$, all cases). Ptarmigan in the Rocky Mountains ingested higher levels of magnesium, iron, and copper ($z = 3.58231$, 4.2596, 3.983, respectively; $P < 0.01$, all cases).

Discussion

We hypothesized that the plant species consumed by white-tailed ptarmigan would differ between ptarmigan in their natural range in the Rocky Mountains of Colorado and an introduced population in the Sierra Nevada of Colorado, and we found this to be supported by the data. Five plant genera (*Draba*, *Juncus*, *Ranunculus*, *Salix*, and *Sibbaldia*) were common to alpine foraging areas of white-tailed ptarmigan in both mountain ranges. Of these five genera, only *Salix* was a major contributor to both diets, the other genera were sampled in minute amounts, together contributing <1% to the diets of each population. *Salix* dominated the summer diet of the Sierra Nevada ptarmigan (92%), but it ranked low in importance in the summer diet of the Rocky Mountain ptarmigan (3.16%). However, in spring and fall, alpine willow species (*Salix* spp.) dominate diets of white-tailed ptarmigan in the Rocky Mountains (May and Braun, 1972; Braun et al., 1993). When introduced to the Sierra Nevada alpine, white-tailed ptarmigan were confronted with a novel array of plant species from which they had to select an appropriate mixed diet to survive. *Salix anglorum* closely resembles the *Salix* species in the Rocky Mountains, and it is high in protein, thus it is reasonable to propose that the introduced birds focused on this species.

Our second hypothesis, that white-tailed ptarmigan in the two populations would differ in their foraging strategies, was also supported by the data. The Rocky Mountain birds foraged in a relatively random manner on numerous plant species compared to the Sierra

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Nevada ptarmigan that foraged in a relatively selective manner on two species. In the Rocky Mountains, flowers of alpine avens (*A. rossii*) were abundant, high in lipid content, and dominated diets of the ptarmigan. Interestingly, *A. rossii* leaves are also high in phenols that herbivores typically avoid because these secondary compounds interfere with digestion (Freeland and Janzen, 1974; Bryant and Kuropat, 1980). North American pika (*Ochotona princeps*) also consume *A. rossii* leaves, but pikas delay eating this food in cached vegetation until phenolic compounds have degraded to a lower level (Dearing, 1997). The ptarmigan consumed only the flowers of *A. rossii*, which may have lower levels of phenols than the leaves but this has yet to be determined. The selection against Patterson's sage (*Artemisia pattersonii*) by the Rocky Mountain ptarmigan is likely due to the high levels of secondary compounds characteristically present in sage species (Robbins, 1983). The second major food in the diet of the Rocky Mountain ptarmigan, *B. vivipara*, is also consumed by Icelandic ptarmigan (*L. mutus*) and is proposed to be a preferred food because it provides carbohydrates and lipids in a low fiber structure (Gardarsson and Moss, 1970). *Dryas octopetala* and *B. bistortoides* were the next dominant foods in the diet of the Rocky Mountain birds, and contributed to the high carbohydrate content of the diets. Although the ptarmigan exhibited no selection for these foods within foraging patches, these foods were more common in foraging areas than in random areas (as was *B. vivipara*). This indicates that ptarmigan forage randomly on these species within a patch, but each foraging patch may be selected due to its abundance of these species. *Trifolium dasyphyllum* was the food highest in protein in the diet of the Rocky Mountain ptarmigan, but no strong selection was evident for this species. This is puzzling because protein has been suggested as a limiting nutrient determining the diet selection of other grouse species (*L. lagopus scoticus* [Moss, 1967], *L. mutus* [Moss, 1968], *Tetrao urogallus* [Pulliainen, 1970]). However, protein in the diets of the white-tailed ptarmigan studied exceeded levels required by many gallinaceous species (protein levels of commercial pheasant and turkey foods range from 16 to 24%; Patrick and Schaible, 1980), thus, protein may not be limiting for white-tailed ptarmigan in the Rocky Mountains. Studies of spruce grouse (*Dendragapus canadensis*) have also shown no selection for protein-rich foods, and it has been suggested that protein may not be limiting for these species (Pendergast and Boag, 1971).

In comparison with the Rocky Mountain population, white-tailed ptarmigan in the Sierra Nevada foraged in a highly selective manner. Regardless of availability, dwarf willow leaves (*S. anglorum*) were the major food in the diet of every ptarmigan in the Sierra Nevada, and these birds selected foraging areas with high abundances of dwarf willow. In addition to dwarf willow, relatively constant amounts of sedge (*C. jonesi*) seed heads were included in every diet. The Sierra Nevada ptarmigan may consume sedge as a complementary food due to its carbohydrate and lipid content, nutrients that are low in the high protein dwarf willow.

Although both populations maintained mixed diets (eating foods with differing nutrient content, or complementary foods), our third hypothesis, that the energy and nutritional content of the diet would differ, was not entirely supported by the data. Energy content of the diets was nearly identical, in spite of the differences in plant species eaten. However, the manner in which the birds met their dietary energetic needs differed between the populations, resulting in differing nutrient intake. Lipid intake did not differ significantly, but the Rocky Mountain population consumed a diet higher in carbohydrate while the Sierra Nevada populations ingested a diet higher in protein. Furthermore, the Rocky Mountain ptarmigan appeared to select foraging areas with foods high in carbohydrates while the Sierra Nevada birds selected foraging areas with protein-rich food. Reasons for these differences in selectivity have yet to be determined and provide opportunities for further investigations. All individuals in both populations exhibited sampling behavior, ingesting a few bites from a wide variety of species. Sampling a wide variety of items is characteristic of the foraging behavior of white-tailed ptarmigan chicks (May, 1975). As adults, white-tailed ptarmigan retain sampling behavior, which may aid them in learning about food sources that vary locally and seasonally in the alpine tundra. Sampling behavior may have enhanced the ability of white-tailed ptarmigan to identify a suitable mixture of foods in the novel plant communities of the Sierra Nevada alpine. Ptarmigan in the Sierra Nevada were successful in obtaining diets that allowed for their survival and reproduction, as evidenced by the fact that their productivity did not differ significantly from white-tailed ptarmigan productivity in natural population in Colorado and Montana a decade after being introduced (Clarke and Johnson, 1990). However, game hunting has now extirpated the population in the Hall Natural Area of the Sierra Nevada (pers. obs.), which appeared to have no negative impacts on native plant and animal communities unlike many introduced species.

In the highly variable alpine tundra environment, behavioral plasticity in foraging may play an important role in monitoring changing resources (Klopfer and MacArthur, 1960; Westoby 1978, Morse, 1980, Clark, 1982, Karasov, 1985), as illustrated by the contrasting foraging behaviors of white-tailed ptarmigan in the Rocky Mountain and the Sierra Nevada, and by their common sampling behavior. Whether selective pressures to monitor seasonally changing food resources have influenced foraging behaviors of other tundra herbivores in a similar manner is a question for further investigation.

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