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Seasonal Variation in Diet of a Marginal Population of the Hispid Cotton Rat, *Sigmodon hispidus*

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ABSTRACT

Cotton rats live in oldfields, habitats with a variety of mostly herbaceous plants. Based on other studies, the hispid cotton rat, *Sigmodon hispidus*, eats many kinds of herbaceous plants but grasses predominate. In contrast, our population of cotton rats ate many monocots but mostly they were not grasses. Our study sought to determine the diet of the cotton rat in eastern Virginia, near the northern limit of distribution on the Atlantic Coast. Fecal samples, collected each month during an on-going capture-mark-release demographic study of the rodent community, were analyzed using a standard method. A greater variety of foods (including insects) was eaten in the summer and autumn than in winter and spring. In winter, when much herbaceous vegetation is standing dead, cotton rats supplemented their diets with pine bark. Cotton rats ate significantly greater proportions of monocots in winter and spring, an apparent response to the need for more calories to compensate for greater heat loss. In summer and autumn, cotton rats enhanced their diets with significantly greater proportions of the more nutritious but harder to digest dicots. Reproductive females ate significantly more dicots and less monocots than males and non-reproductive females, whose diets were similar. Key words: cotton rat, diet, fecal analysis, pine bark, plant availability, seasonal variation, *Sigmodon hispidus*

INTRODUCTION

Studies of diet, at their simplest, reveal whether mammals are herbivores, carnivores, omnivores, or consume specialized foods such as ants. When evaluated throughout an annual cycle, dietary studies also can indicate the role of that species in its community and how diet may change with the seasons, with the changing energy requirements of reproduction, impending migration or hibernation (Parker and Bernard, 2006). Diet can be assessed by direct observation, feasible primarily for large diurnal mammals, or by analysis of the contents of stomach or feces (Colgan et al., 1997).

Previous studies of the diet of the hispid cotton rat (*Sigmodon hispidus*), conducted using fecal analysis, have shown that this rodent is mostly herbivorous but occasionally also consumes insects. Examined in coastal Texas throughout an annual cycle (Kincaid and Cameron, 1985) and in western Kansas in the summer (Fleharty and Olson, 1969), the latter representing a marginal population, the diet of cotton rats varies greatly due to the large variety of plant species in their habitats and to their differences in nutrient

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content, secondary plant compounds, palatability and digestibility (Randolph et al., 1991). These features undoubtedly change during the year, with foods likely of poorest quality and lowest amount during the winter months. Diet may reflect the availability of plant species, but often it does not (Randolph et al., 1991).

Cotton rats consume mostly monocots, especially grasses, but also eat dicots (Kincaid and Cameron, 1985). Laboratory studies show that monocots are digested more rapidly and thus provide calories easily, whereas dicots are more nutritious but take longer to digest (Randolph et al., 1991). These factors can contribute to the differential selection of food plants by cotton rats of different reproductive states living in different months of the year. Knowledge of the diet of the cotton rat near the northern limit of distribution in the mid-Atlantic region will permit comparisons with more central and other peripheral populations. Using fecal samples collected throughout the year, our study sought evidence of seasonal variation in food selection, including information on the dominant plant species consumed in different seasons. We also compare differences in food selection among males, non-reproductive females, and reproductive females.

MATERIALS AND METHODS

Study Area

The study site was an 11-ha tract owned by The Nature Conservancy in southern Chesapeake, Virginia. The flora consisted of several monocots, including *Juncus effusus* and *J. tenuis* (soft rushes), *Schizachyrium scoparium* (little bluestem), *Allium vineale* (field garlic), *Carex* spp. (sedges), *Panicum* spp. (switchgrass), *Scirpus cyperinus* (a sedge, wool-grass), and *Microstegium vimineum* (Nepalese browntop grass). Also present was a variety of dicots: *Symphotrichum pilosum* (awl-aster), *Solidago* spp. (goldenrods), *Solanum carolinense* (horse nettle), *Campsis radicans* (trumpet creeper), *Lonicera japonica* (Japanese honeysuckle), *Apocynum cannabinum* (hemp-dogbane), *Eupatorium capillifolium* (small dog-fennel), *Rubus allegheniensis* (blackberry), and *Ambrosia artemisiifolia* (common ragweed). The site was being rapidly invaded by loblolly pine (*Pinus taeda*) trees that gradually decreased the amount of herbaceous ground cover, originally dominant. In the wettest areas, soft rushes, wool grass and asters were the dominant plants. In addition to cotton rats, other small mammals in the community, in order of their decreasing abundance, were: *Microtus pennsylvanicus* (meadow vole), *Reithrodontomys humulis* (eastern harvest mouse), *Oryzomys palustris* (marsh rice rat), *Mus musculus* (house mouse), and *Blarina carolinensis* (southern short-tailed shrew).

Field Methods

A 1-ha grid, consisting of eight rows of traps with eight stations at 12.5 m intervals along each row, was placed in a grassy section of the field in December 2002. Every coordinate had two Fitch live traps (Rose, 1994) that were baited with birdseed and filled with polyfill as insulation in the winter months. The traps were set one afternoon and then checked for three consecutive mornings each month. Half sheets of copy paper, placed under the mesh when setting traps, collected feces on the first morning of trapping. The feces from each animal were folded in the paper, which was labeled with information on sex, weight, date, and tag number, and then stored in a freezer. Fecal samples from 53 cotton rats, with 10-15 samples per season, were analyzed. The seasons were defined as autumn (September-November), winter (December-February),

spring (March-May) and summer (June-August).

Because the cotton rats analyzed in our study were part of an ongoing capture-mark-release study (which followed the guidelines of the American Society Mammalogists for the use of wild mammals in research: Gannon et al., 2007), analysis of diet using only fecal samples was possible. For each animal, we also recorded information on its reproductive status. For males, the testes were recorded as scrotal (reproductive) or abdominal (not reproductive). For females, reproductive information included if pregnant, whether vagina was perforate or not, nipple size (small, medium, and large), and the condition of pubic symphysis (closed, slightly open, or open). Together these features permit an assessment of reproductive condition (McCrary and Rose, 1992).

Lab Analysis of Plant Parts and Fecal Samples

Each month during spring and summer of 2006, plants were collected and identified in the field; identifications were verified by a plant expert (Dr. Rebecca Bray and Jay Bolin) in the department. Later, parts of the plants were used to make reference slides for each species, using the procedures of Davitt and Nelson (1980). Pieces of a plant were placed in a lactophenol-blue stain for 7 d and then macerated in a Waring blender for 3-5 min. The smallest plant particles were removed from the surface of the water using a tiny wire loop, placed on a microscope slide (two slides per reference plant), and then dried on a hot plate. Once the slide was dry, a mounting medium and coverslip were added to create a semi-permanent reference slide for each plant species (Davitt and Nelson, 1980).

Five to six fecal pellets per sample were also subjected to the lactophenol-blue stain, then ground with mortar and pestle, the smallest pieces again were looped from the surface of the water, mounted on a slide and dried. Two slides per sample were prepared as before. Twenty-five random microscope fields were examined per slide (50 fields/sample). If 100X magnification was inadequate for identification, higher magnification was used.

The reference slides were used to identify the plant fragments in each fecal sample. Unique micro-anatomical features, such as epidermal hairs, size/shape of cells, trichomes, and stomates were used to identify the plant pieces (Sparks and Malcheck, 1968). For each fecal sample slide all particles of each plant species (plus unidentifiable pieces) were counted in each field of view. After these values were summed in all 50 fields, these totals were divided by the total number of fragments of all the species (and unidentifiable parts) per sample and then multiplied by 100 to give percent frequencies of species consumed by the cotton rat (Holecheck and Gross, 1982). This method resulted in a list of the plant species in each fecal sample and their relative proportions, expressed as percent frequencies. Five categories were used: unknown (unidentifiable fragments caused by excessive digestion or distortion), monocots, dicots, pine bark and insects. This information was then merged with information on the sex, reproductive status of the animal and season to give a picture of the changing diet of the cotton rat throughout the year.

Fecal samples used in the analysis were collected from September 2004 through August 2005. Plant abundances were not determined due to the rapid succession in the oldfield between the time the fecal samples were collected and the time that plant samples were collected (spring and summer 2006).

Data analysis

All statistical tests for the diet analysis were performed using SPSS for Windows

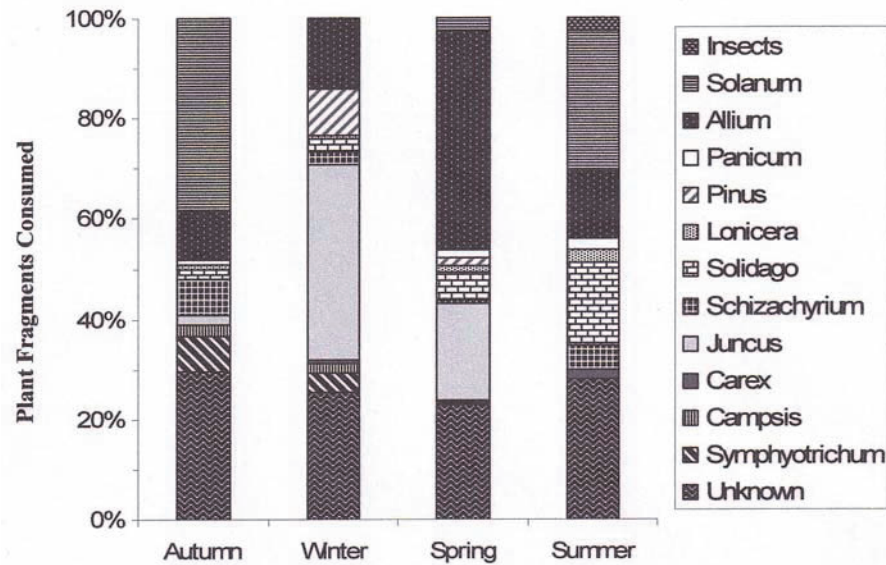


FIGURE 1. Percentages of insects and plant species identified in fecal samples in each of four seasons ($n = 53$: 10-15 per season).

2005, version 14.0, with significance levels of $P < 0.05$ (SPSS Inc., Chicago, Illinois). The percent frequencies of diet were tested for normality and homogeneity of variances using Kolmogorov-Smirnov and Shapiro-Wilk tests of normality. The unidentifiable components, monocots, and dicots for the seasons were normally distributed but due to the multiple zeros recorded for pine bark and insects, those variables were not normally distributed. After multiple transformation attempts, the tests of normality still could not be met satisfactorily for pine bark and insects. Therefore, percent frequencies were used in a general linear model (GLM) multivariate analysis (MANOVA) to compare the diet composition between season and sex in relation to major food types. If there was a significant effect from either the season or sex on a major food type in the GLM MANOVA, a one-way ANOVA Ryan-Einot-Gabriel-Welsch-F test (REGWF) was performed to test the significance of each major food type individually against each season or sex.

RESULTS

Effects of Season on Percent Food Consumption

The percent of unknown plant fragments was relatively constant across the four seasons, ranging from 22-29% (Fig. 1). The following were the primary foods consumed: monocots (*Juncus*, *Schizachyrium*, *Allium*, *Carex*, and *Panicum*), dicots (*Symphyotrichum*, *Solidago*, *Solanum*, *Campsis*, and *Lonicera*), pine bark, and insects; these four groups were used in analysis.

The most important plant species varied among seasons (Fig. 1). In autumn, *Solanum* represented 39% of the diet, with *Symphyotrichum*, *Schizachyrium*, and *Allium*

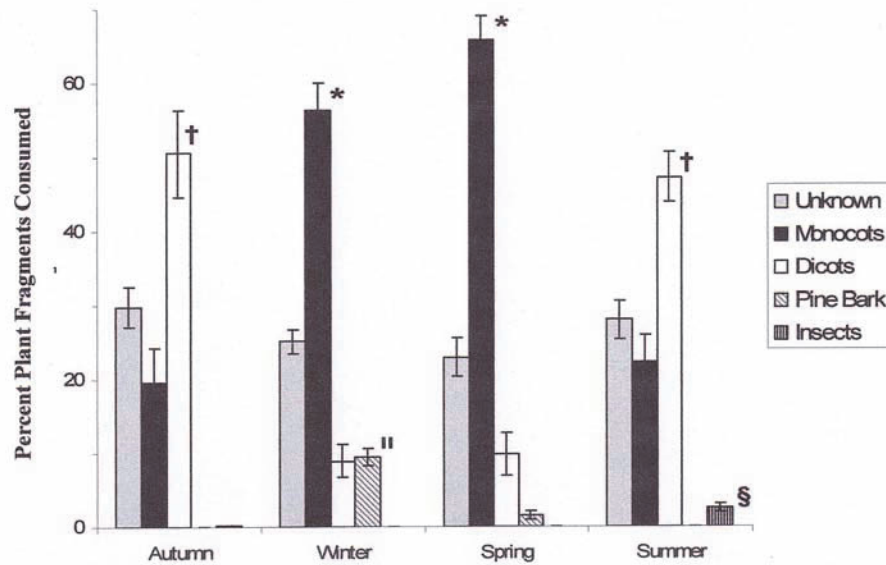


FIGURE 2. Percentages (mean \pm 1 SE) of plant fragments, and insects, separated into food categories eaten for each season. The following symbols are used: † proportions of dicots consumed were significantly greater in summer and autumn than winter and spring ($P < 0.01$), * proportions of monocots consumed were significantly greater in winter and spring than summer and autumn ($P < 0.01$), †† proportions of pine bark consumed was significantly greater in winter than spring, and ‡ proportions of insects consumed was significantly greater in summer than autumn ($P < 0.01$).

as minor (7-10%) components. During winter, the diet primarily consisted of *Juncus* (39%), *Allium* (14%), and pine bark (9%). In spring, *Juncus* and *Allium* were dominant again, but their proportions were reversed: 44% for *Allium* and 20% for *Juncus*. Finally, in summer, a greater variety of plants was eaten, with *Solanum*, *Solidago*, and *Allium* consumed the most at 28%, 17%, and 14%, respectively. Despite its availability, *Juncus* was not eaten in summer, perhaps due to the variety of other plant species available then.

In winter and spring, monocots were 56% and 66% of the identifiable diet and dicots were only 9% and 10%, respectively (Fig. 2). The greater use of monocots in winter and spring versus summer and autumn was significant based on the post-hoc REGWF test ($P < 0.01$). A significantly greater proportion of pine bark was eaten in the winter than in spring ($P < 0.01$). In summer and autumn, dicots made up 47% and 50%, respectively, seasons when monocots constituted less than 25% of the diet (Fig. 2). This preference for dicots in the summer and autumn was significantly greater ($P < 0.01$) than in the winter and spring. Significantly ($P < 0.01$) more insects were eaten in summer (2.5%) than in autumn (0.1%); both are seasons of greatest availability.

Effects of Sex on Percent Food Consumption

Over the year, males ($n = 18$) ate 43% monocots and 30% dicots and non-

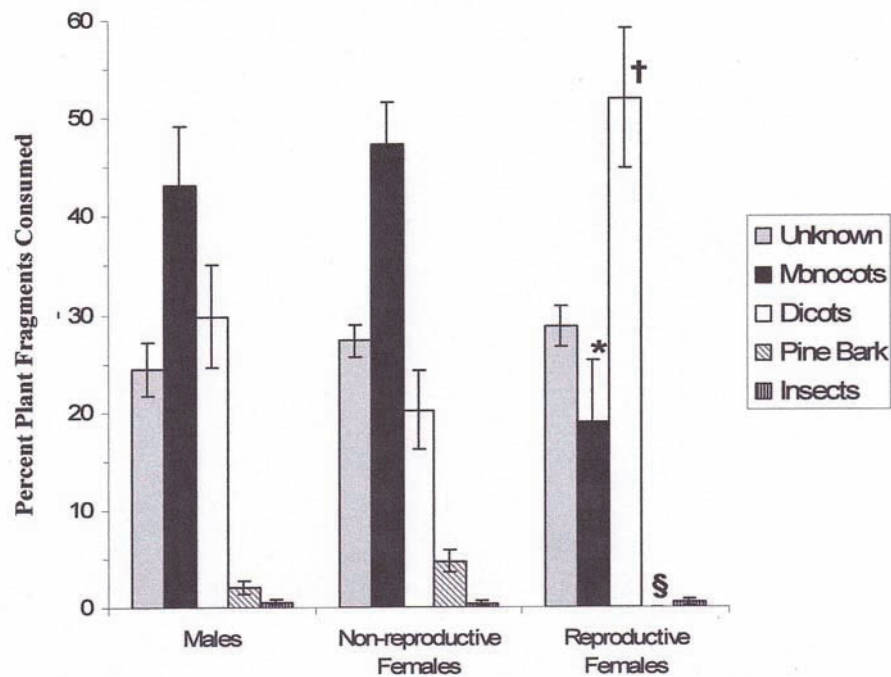


FIGURE 3. Percentages (mean \pm 1 SE) of plant fragments, and insects, separated into food categories for males (M), non-reproductive females (NRF) and reproductive females (RF), with $n = 18$, $n = 27$, and $n = 8$, respectively). The following symbols are used: *proportions of monocots consumed by RF was significantly less than M and NRF ($P < 0.05$), † proportions of dicots consumed by RF was significantly greater than M and NRF ($P < 0.05$) and § proportions of pine bark consumed by RF was significantly less than M and NRF ($P < 0.05$).

reproductive ($n = 27$) females consumed similar proportions, at 47% and 20%, respectively (Fig. 3). However, reproductive females ($n = 8$) consumed 19% monocots and 52% dicots. Post-hoc tests showed that reproductive females ate significantly ($P < 0.05$) less monocots and more dicots than males and non-reproductive females. Males and non-reproductive females consumed significantly ($P < 0.05$) more pine bark (2% and 4.7%, respectively) than reproductive females, which ate none. The amount of insects consumed, never greater than 1%, did not differ among the three groups. Males and non-reproductive females consumed relatively similar proportions of monocots, dicots, pine bark, and insects ($P > 0.10$).

DISCUSSION

Cotton rats are short-lived animals that grow rapidly with an average lifespan varying from 2-3 months depending on location (Cameron and McClure, 1988). Due to the short lifespan, cotton rats cannot substantially benefit from having selected or avoided certain plants earlier in the year (Randolph et al., 1991). At our site, they consumed varying proportions of 10 common herbaceous plants, a few insects when

available and at one time of the year, pine bark. During the year, different monocots and dicots were eaten, presumably depending upon their availability, palatability and nutritional values.

Proportions of monocots, dicots, pine bark and insects eaten varied with the season. Monocots typically were eaten more in the winter and spring, when they represented greater than 50% of the identifiable diet (Fig. 2). Especially in winter, relatively little living green herbaceous vegetation except *Allium* and *Juncus* (both monocots) was available (Fig. 1). During winter and spring, when the food selection likely was limited, cotton rats consumed pine bark to supplement their diets (Fig. 1). Even though pine bark contains noxious resins and tannins, cotton rats at our site consumed it in relatively large amounts, especially in late winter (Fig. 2). Cotton rats ate pine bark at a time when nutrient-rich sap is rising from the roots and when food quality probably is lowest in overwintering herbaceous plants. We assume they are improving their diets by eating bark. Other rodents known to eat the bark of conifers, not necessarily at one time of the year, include the Abert's squirrel (*Sciurus aberti*), which eats phloem and cambium of the bark of the ponderosa pine in western North America as the primary winter food (Snyder, 1992) and in the United Kingdom the introduced gray squirrel (*Sciurus carolinensis*) strips and eats pine bark, mostly in May-July, when bark is stripped most easily (Dagnall et al., 1998).

In summer and autumn the reverse pattern was observed, with cotton rats eating significantly more dicots than monocots; dicots comprised ca. 50% of their diet then (Fig. 2). The most common dicots eaten during the summer and autumn were *Solanum* (28 and 39%, respectively), and *Solidago* (17 and 2%) (Fig. 1). Although pine bark was not found in fecal samples from summer and autumn, insects were (Fig. 2). Kincaid and Cameron (1982) believed insect consumption, highest in the summer, was by incidental ingestion, but our results suggest active insect consumption. Of the 25 cotton rats sampled in summer and autumn, 10 (40%) had eaten insects (Fig 2). Active eating of insects is also supported by high infestation rates (25-73% per month, R. Rose, unpublished) in local cotton rat populations of the stomach worm, *Mastophorus muris*, for which insects such as crickets, grasshoppers, and others are the intermediate hosts.

Many studies (e.g., Fleharty and Olson, 1969; Kincaid and Cameron, 1985; Randolph and Cameron, 2001) have reported that cotton rats primarily eat grasses. In Kincaid and Cameron (1985), grasses were highly dominant, comprising the majority of foods consumed in most seasons and 74% of the diet across the year. After learning that foods of higher nutritional content, such as dicot leaves, were typically eaten in summer, Randolph and Cameron (2001) concluded that cotton rats had to compensate for the longer handling time of dicots by trying to decrease the search time. Fleharty and Olson (1969), in a summer-only study in Kansas, also found that dicots were consumed more than grasses then. The food consumed in the highest percentage volume was *Triticum aestivum* (wheat, a grass) at 20%, but in aggregate, forbs comprised 48% of summer diet (Fleharty and Olson, 1969). In our study, dicots were eaten in large amounts in summer and autumn, whereas monocots (including grasses) were consumed more in the winter and spring.

Kincaid and Cameron (1985) found that grasses were consumed most frequently during autumn and winter in the Texas coastal prairie, whereas dicots were consumed more in spring and summer. This is a seasonal shift in pattern compared to our results,

and is probably due to the geographic variation in flowering phenology of food plants. Further, our dominant and important plant species (*Juncus*, *Solanum*, *Allium*, *Solidago*) were absent in the Kansas study and, except for *Solidago*, in the Texas study too. All three studies showed dicots were consumed more than monocots in the summer and the opposite pattern in the winter. However, we never found grasses to be dominant plants in the diet. Of the grasses, *Schizachyrium* was consumed the most in autumn at 7% and *Panicum* the most in summer at 2%. Consequently, in our study grasses comprised only 5% of the average cotton rat diet, which is drastically different from the 74% reported by Kincaid and Cameron (1985). Besides these differences, pine bark, previously unreported as food of cotton rats, was an important component in the diet for a short period at the end of winter. Thus, our study shows the dietary flexibility required of small mammals that can continue to expand their distribution, as *Sigmodon hispidus* has done for the past century (Cameron and McClure, 1988).

Among the factors that determine which species of plants a cotton rat consumes are stage of growth, palatability (Flehart and Olson, 1969), and search, handling and digestion times (Randolph and Cameron, 2001). Dicots are high in protein but require longer handling times than monocots, whereas monocots have shorter handling times but are not as nutrient rich as dicots (Randolph et al., 1991). Randolph and Cameron (2001) found that differences in both search and handling times played a role in diet selection among seasons. This likely was the case in our study because cotton rats on our grid could find monocots easily during all seasons, with *Juncus* and *Allium* being widely distributed and common on the grid and among the few green foods available in winter and early spring. Accessible foods in winter and spring were mainly monocots, which are easy to break down and convert into energy rapidly. In summer, when cotton rats do not lose as much energy to heat loss as in other seasons, they can afford to eat foods that take longer to find and digest, such as dicots, because they do not need to catabolize energy so rapidly from food then, except perhaps for lactating females.

When examining food consumed over the entire year, a few differences were noted between the sexes (Fig. 3). Males and non-reproductive females consumed 2% and 4.7% of pine bark, respectively. (Pine bark was being consumed in late winter and early spring before females were actively breeding.) Randolph et al. (1991) reported that seasonal diets of males and non-reproductive females were similar except in winter. Our sample sizes were too small to examine differences between sexes among seasons, but males and non-reproductive females had similar diets across the year. Furthermore, reproductive females ate more dicots (52%) than either non-reproductive females or males (20 and 30%, respectively; Fig.3). Also reported by Randolph et al. (1991), this behavior suggests that reproductive females take an active role in meeting the nutritional requirements of pregnancy and lactation.

Randolph et al. (1995) reported that cotton rats fed lab chow had enough energy to meet reproductive requirements, but females in the field had levels of protein and phosphorus too low to meet the demands required for reproduction in both autumn and winter. Females need more energy during lactation than in pregnancy and are constantly balancing between energy lost through heat dissipation and reproductive costs. Due to the high nutritional demands of reproduction, it is important that females eat foods high in protein, which may be the reason reproductive females in our study ate relatively more dicots than non-reproductive females. In an experimental field

study in Texas during which high-protein foods were introduced into some natural habitats, cotton rats chose habitats with high quality foods even when covering vegetation was low, indicating an ability to evaluate food quality (Eshelman and Cameron, 1996). Males and non-reproductive females can afford to be less choosy about the foods they consume because they do not need as much energy (Randolph and Cameron, 2001), which may explain their similar diets.

In conclusion, cotton rats in eastern Virginia exhibited significant seasonal variation in food selection, including the unexpected consumption of pine bark and much lower proportions of grasses eaten than reported for other geographic populations. Significant diet differences were observed between reproductive females and either males or non-reproductive females. The catholic diet of the hispid cotton rat probably has contributed to its range expansion in the last 100 years, including into southeastern Virginia, where its path northward currently is blocked by the Chesapeake Bay and its associated large rivers.

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