



Adult Versus Juvenile American Red Squirrels Feeding on Eastern American Black Walnuts

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Abstract

American red squirrels (*Tamiasciurus hudsonius*) consume a wide variety of foods including the nutmeats of eastern American black walnuts. However, the thick, hard shells require considerable gnawing to access the nuts inside. This study compared the efficiency of black walnut nutmeat extraction between adult and juvenile squirrels by measuring the sizes of the openings gnawed by different squirrels feeding on nuts from a single source tree. The remains of walnut shells fed on by an adult female and two of her juvenile offspring were collected from middens under three separate trees and measured (shell height, width, dimensions of gnawed openings). Shells fed on by squirrels were similar in length but significantly larger in width than intact shells, although there was no difference in size selection between the adult and the two juveniles. Gnawed openings (one on each side of the shell) differed in size among squirrels, with the adult producing significantly smaller openings (median = 234 mm²) than the juveniles (medians = 272 and 304 mm²) to extract all nutmeats. Two openings per shell represented a combined 15% to 19% (median values) of the total nut surface areas. These results suggest that red squirrels may become more efficient at extracting walnut nutmeats via smaller openings as they gain experience with this food source.

Keywords: Red Squirrel; *Tamiasciurus hudsonicus*; Black Walnuts; *Juglans nigra*; Feeding Efficiency; Nutmeats

Introduction

American red squirrels (*Tamiasciurus hudsonius*) range across Canada and the USA, consuming a variety of plant- and animal-based foods [1-3]. The species is well known for long-term use of the same locations to extract seeds from the cones of various conifers or nutmeats from various tree nuts, often creating large conspicuous middens from the discarded materials [1,3-6]. Some foods such as tree leaf buds, flowers, and small seeds are relatively easy to process, requiring little experience or handling time to acquire nutrients [7], whereas others such as large nuts may require significantly more effort and/or experience to access the desired portions [8,9].

Within the eastern and midwestern USA, the range of red squirrels overlaps with that of the eastern American black walnut (*Juglans nigra*) [10,11]. Black walnut trees frequently produce abundant annual crops of relatively large (4–5 cm in diameter) fruits that are consumed as food by a variety of North American tree squirrel species (red squirrels, eastern gray squirrels *Sciurus carolinensis*, fox squirrels *Sciurus niger*) [9,12-15]. The fruits consist of a fibrous outer layer covering a thick, hard woody nutshell (Figure 1A) which contains the nutrient-rich nutmeat. Squirrels first remove the outer layer with their teeth and clawed front feet before using their incisors to gnaw through the woody nutshell to gain access the nut (N. Mundahl, personal observation).

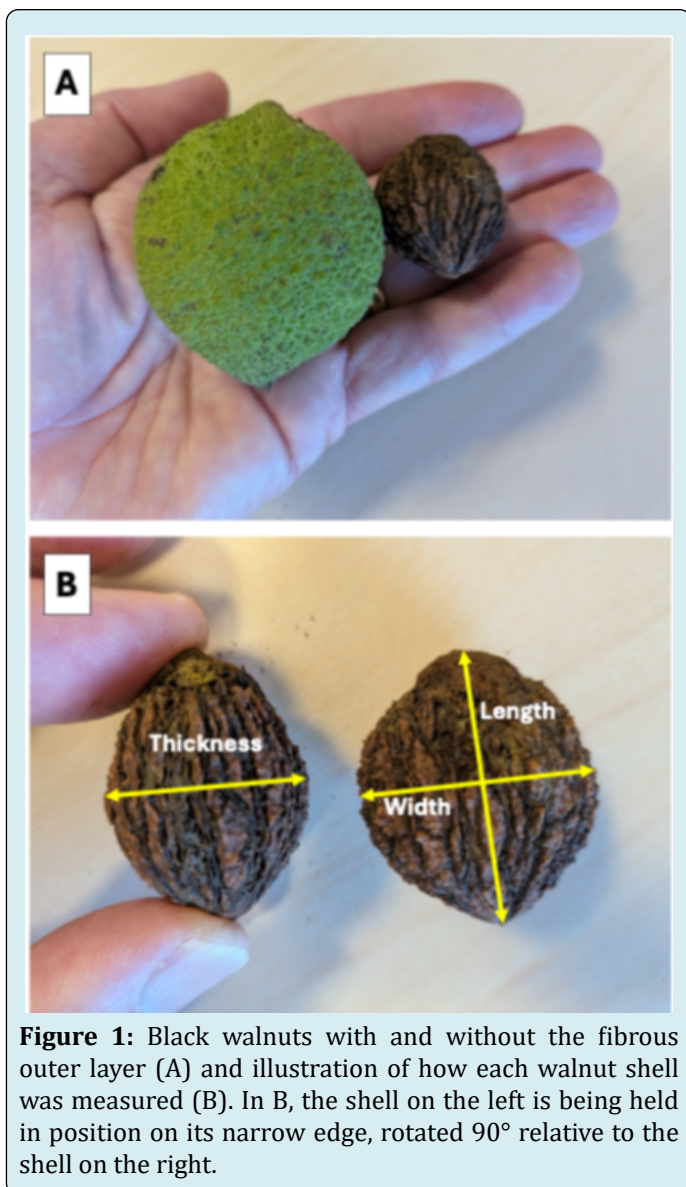


Figure 1: Black walnuts with and without the fibrous outer layer (A) and illustration of how each walnut shell was measured (B). In B, the shell on the left is being held in position on its narrow edge, rotated 90° relative to the shell on the right.

Although tree squirrels may prefer and regularly consume black walnuts [14-16], those walnuts may comprise only a minority of squirrel diets despite their potential abundance [1,16,17]. Squirrels typically experience longer handling times when eating black walnuts than when feeding on other types of nuts [9,18-20], indicative of the degree of difficulty experienced by squirrels in accessing the walnut nutmeat inside the hard shell [9]. This can make black walnuts an energetically inefficient food resource despite their high nutritional value [9]. However, at least one tree squirrel population with long-term (80 to 100 years) exposure to black walnuts as food has displayed gradual, long-term changes (or evolution) in cranial morphology (i.e., skull size, jaw elongation, mandibular characters) that allow the squirrels to feed more effectively and efficiently on black walnuts [9].

Rather than searching for other foods that may be easier to access than black walnuts, tree squirrels faced with a high abundance of walnuts may instead attempt to reduce walnut handling times to increase the rate of food intake. Previous studies have shown that a squirrel's nut handling times can decrease substantially with experience [8], allowing for more nuts to be processed and consumed per time period. Squirrels also may decrease handling times by exposure to an experienced squirrel feeding on nuts, learning more efficient handling strategies by simple observation rather than via trial and error in isolation [8]. However, enhanced handling via learning may be restricted primarily to juvenile squirrels [21].

Tree squirrels are known to use specific behaviors to assess the size and/or quality of nuts prior to consumption [13]. Potentially, there also may be various squirrel feeding behaviors or actions that could reduce black walnut handling time. These might include alternative strategies for removing the fibrous outer layer, selecting walnuts of specific sizes most suitable for consumption, accessing the nutmeat through different shell surfaces, or creating access openings of different sizes and shapes. Many of these could be evaluated via examination of black walnut shells fed on by squirrels.

In this study, a family of American red squirrels (adult mother and two juveniles) feeding on black walnuts in a residential neighborhood provided an opportunity to examine the role of experience in affecting how squirrels opened walnut shells to remove the nutmeats. By each squirrel feeding on walnuts and creating individual middens in separate locations, the walnuts fed on by each squirrel could be examined and assessed to determine whether they differed from one another. I hypothesized that the experienced adult female would be more efficient at accessing the nutmeats within each walnut by 1) selecting a specific (i.e., most energetically efficient) size of walnut to eat [13], 2) accessing the nutmeat consistently and most efficiently through the same side(s) of the shell [8], and 3) creating significantly smaller gnawed openings to accomplish complete nutmeat removal compared to her two inexperienced offspring. I suspected that these together should translate directly to reduced handling time and increased rate of nutrient intake by experienced adult squirrels compared to their inexperienced offspring.

Study Site and Squirrel Behavior

The study site was a residential neighborhood in suburban Winona, MN, USA (44°00'47.33" North, 91°37'47.55 West). A single mature black walnut tree was the source of all walnuts eaten by resident red squirrels. Other nearby seasonal food source trees included a red oak (*Quercus rubra*; 21 m from

the walnut tree), a silver maple (*Acer saccharinum*; 30 m), a common hackberry (*Celtis occidentalis*; 39 m), two apple trees (*Malus* spp.; 28 and 61 m), two blue spruce trees (*Picea pungens*; 35 and 37 m), and a swamp white oak (*Quercus bicolor*; 39 m). The red squirrel breeding drey (i.e., nest) was located in one of the spruce trees. The ground in this area was mostly mowed turfgrass, landscaped flower beds, and a vegetable garden.

After weaning her two offspring, the adult female red squirrel largely took up residence in and around the walnut tree and actively excluded her offspring from the tree throughout the autumn months. Although both juveniles were able to gather some fallen walnuts from the ground near the edge of the tree's canopy or "steal" them from the adult's cache in a nearby woodpile, their mother prevented them from collecting enough walnuts to produce any noticeable caches. The adult female ate walnuts almost exclusively while sitting at the base of the walnut tree or on its lower branches, creating a midden of outer walnut husks and emptied shells. The two juveniles created their own separate middens at the bases of the maple tree (juvenile 1) and the hackberry tree (juvenile 2), respectively.

On 27 November 2015, I observed the adult female red squirrel locate and pick up a black walnut (already with the fibrous outer layer removed) near the base of the walnut tree. It climbed upward to the first horizontal branch to eat the nut. It spent 7 minutes and 54 seconds eating the nut before climbing down and dropping the now empty shell in its midden at the base of the tree. The nut displayed a single gnawed opening (roughly rectangular) across each of the two flattened sides of the shell.

Materials and Methods

Walnut Collections and Measurements

Emptied walnut shells were collected from each of three red squirrel middens: 1) the one produced by the adult female beside the walnut tree, 2) the midden made by juvenile 1 at the base of the maple tree, and 3) the one belonging to juvenile 2 beside the hackberry tree. Only emptied shells with two gnawed openings were retained (see below). Some shells were judged to have been emptied by eastern gray squirrels (*Sciurus carolinensis*); gray squirrels produced openings that were larger and dumb-bell shaped compared to the smaller and rectangular openings created by red squirrels (Figure 2A). These were discarded and not included in analyses. Additional unopened walnuts, with the outer layer of husk removed but the entire shell still intact, were collected throughout the area to make size comparisons to the predated nuts.

I originally hypothesized that juvenile red squirrels would access walnut nutmeats by gnawing through a variety of shell surfaces, whereas the adult female squirrel would consistently open shells via a very limited number (one or two) of surfaces that resulted in the most efficient nut extraction. However, it quickly became evident that both adult and juvenile red squirrels always gnawed two openings in every shell, one on each of the flattened sides, to access the nutmeat. Consequently, I focused this study on the sizes of nuts selected for consumption and the size of holes gnawed in shells to extract nutmeats.

For each emptied shell, its length and width (nearest 0.1 m using a dial calipers; Figure 1B) were measured and the area of the gnawed opening on each side of the nut (roughly rectangular; Figure 2B) was estimated by measuring the length and width of each opening and multiplying these to determine the area of the opening. Overall shell height and width were used to estimate the total area of the shell prior to predation, so that the size of the gnawed openings could be expressed as a percentage of total shell surface area.

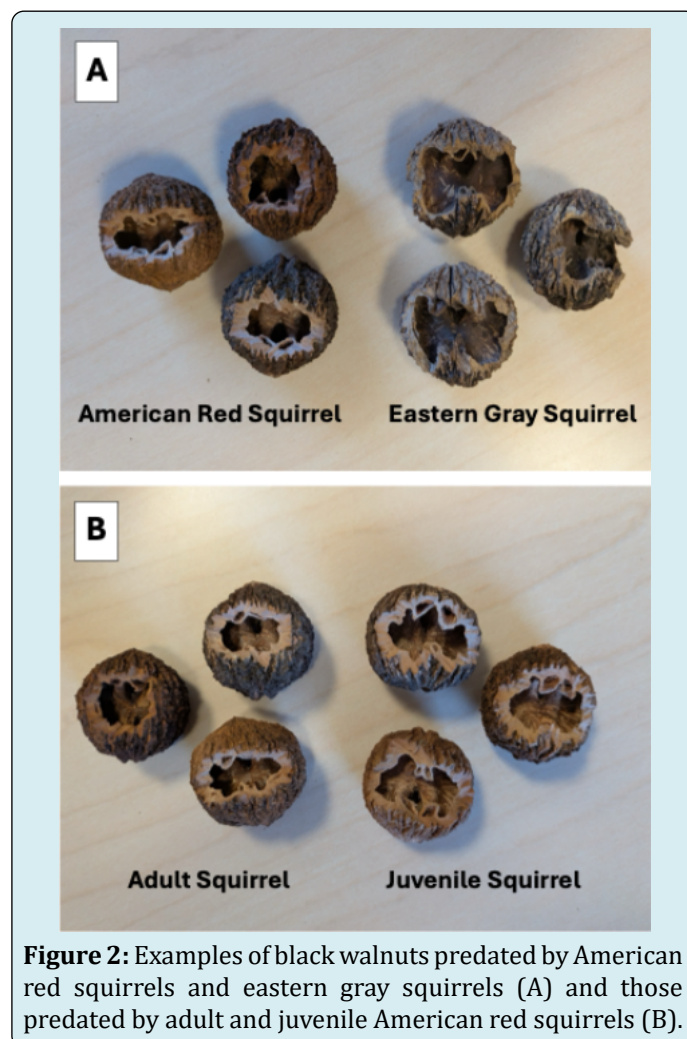


Figure 2: Examples of black walnuts predated by American red squirrels and eastern gray squirrels (A) and those predated by adult and juvenile American red squirrels (B).

Because walnut shells were shaped like flattened and elongated spheroids, three measurements (length, width, and thickness, each to the nearest 0.1 mm using a dial calipers; Figure 1B) were made on each of the intact walnuts to estimate the total, smoothed outer surface area of the shell. These three measurements (each roughly a diameter measure) for each shell were first divided by 2 to produce radii, then averaged to produce a single radius value, and finally used in the standard formula for calculating the surface area of a sphere:

$$\text{surface area (in mm}^2\text{)} = 4\pi r^2$$

where r is the average radius in mm. This allowed a total surface area to be estimated for each intact walnut shell. Mass of each intact nut also was measured (nearest 0.01 g) on a digital balance (Mettler-Toledo PB3002-S/FACT CLASSIC Plus, Mettler-Toledo, LLC, Columbus, OH, USA).

Because predated shells had been opened in a manner that considerably reduced overall shell thickness, the surface areas, lengths, and widths of intact nuts were used to develop an equation that could be used to predict surface areas of predated nuts by using only their heights and widths:

$$y = (A * \text{length}) + (B * \text{width}) + C$$

where y = surface area, A and B are multipliers, and C is a constant.

Red Squirrel Tooth Measurements

The sizes of the gnawed openings on walnuts were compared to the sizes of teeth (i.e., incisors) of red squirrels. To obtain measurements on the incisors of red squirrels, I located four red squirrel skulls in the mammal museum collections at Winona State University, Winona, MN, USA, and at Saint Mary's University of Minnesota, Winona, MN, USA. No information was available on the age (i.e., juvenile versus adult) of the squirrels when the skulls were collected. Incisors were measured to the nearest 0.1 mm with a dial calipers. Measurements included lengths of both upper and lower incisors (one upper and one lower measurement) plus three measurements of the combined widths (basal, middle, distal) of both the uppers and lowers, for a total of eight measurements of dentition on each skull.

Data Analyses

To determine if the red squirrels were selective in the nuts they chose to eat, I compared the heights and widths of intact nuts to the dimensions of those consumed by the squirrels using a pair of Kruskal-Wallis tests with the aid of VassarStats: Website for Statistical Computation (vassarstats.net; accessed 6 August 2026). If a significant difference was detected among the intact nuts and any of those eaten by the three squirrels, a Tukey's Honest Significant Difference

(HSD) test (vassarstats.net; accessed 6 August 2026) was used to determine where the difference(s) existed.

I also used a series of Kruskal-Wallis tests to determine if the size of the gnawed openings in the nuts eaten by the three squirrels differed among the animals. One test compared the actual sizes (mm²) of the openings among the squirrels that produced them, another compared the sizes of the individual openings expressed as percentages of the nut's total surface area, and the final test compared the combined total areas of the two openings on each nut expressed as a percentage of total nut surface area. As before, if significant differences were detected among the sizes of openings created by the three squirrels, a Tukey's HSD test was used to determine where the difference(s) existed.

Results

In late November, I collected 111 intact black walnuts from near the walnut tree at the study site. All these walnuts had their outer coverings removed but were otherwise intact; there was no evidence of gnawing by squirrels on any of them. Intact walnuts were slightly (>13%) longer than wide, and average thickness was 74% of average length (Table 1, Figure 1B). Walnut mass averaged 11.5 g (range from 8.3 to 13.7 g), and walnut surface area estimates averaged 3049 mm² (range = 2636 to 3519 mm²) (Table 1).

In addition to the intact walnuts, I collected 220 empty shells from the adult female squirrel's midden, 12 from the midden of juvenile 1, and 31 from the midden of juvenile 2. Walnut lengths did not differ significantly among the groups of intact and predated walnuts (Table 2). However, widths of walnuts eaten by squirrels were significantly greater (about 2 to 3 mm overall) than those that had not been eaten (Table 2). Widths of nuts eaten by the adult female did not differ significantly from widths of those eaten by the two juveniles. Consequently, while both adult and juvenile squirrels selected walnuts to eat that were generally wider than those available for consumption, the adult squirrel did not exhibit size selection that differed from that of the juvenile squirrels.

Variable	Mean±SD
Length (mm)	35.6±1.6
Width (mm)	31.3±1.6
Thickness (mm)	26.5±0.8
Mass (g)	11.52±0.93
Surface area (mm ²)	3049±191

Table 1: Dimensions and masses of intact black walnut shells. Values are means ± one standard deviation of 111 walnuts. Refer to Figure 1B and the text for how shell dimensions were measured.

Nut Category	n	Length (mm)	Width (mm)
Intact nuts	111	35.5 (34.3, 36.9)	31.3 (30.6, 32.1) A
Adult female	220	35.3 (34.2, 36.5)	33.2 (32.1, 34.3) B
Juvenile 1	12	35.1 (34.9, 39.8)	34.3 (33.5, 34.8) C
Juvenile 2	31	35.1 (34.3, 35.9)	33.6 (33.0, 34.7) BC
Kruskal-Wallis <i>H</i>	–	2.49	109.35
<i>p</i>	–	0.48	<0.0001

Table 2: Comparisons of the lengths and widths of intact and predated (by one adult female and two juvenile red squirrels) black walnut shells. Values are medians with 25th and 75th percentiles in parentheses. Sample sizes (n) are included. Results of Kruskal-Wallis tests are shown separately for lengths and widths. Width values not having a letter in common are significantly different from one another (Tukey's LSD test).

The adult female red squirrel created openings on the walnut surfaces with a median area of 234 mm² but both juveniles produced significantly larger (16 to 30%) openings (Table 3, Figure 2B). When expressed as a percentage of total nut surface area, most individual openings and the

two openings per shell were <10% and <20% of nut surface area, respectively (Table 3). Percentage areas (individual or combined) differed significantly only between juvenile 2 and the other two squirrels (12 to 27% larger).

Squirrel	Opening area (mm ²)	Opening % of Surface Area	Combined Openings % of Surface Area
Adult female	234 (206, 270) A	7.4 (6.5, 8.4) A	15.0 (13.3, 16.8) A
Juvenile 1	272 (233, 319) B	8.4 (7.1, 9.8) A	16.4 (14.9, 19.7) A
Juvenile 2	304 (262, 352) C	9.4 (8.1, 10.7) A	19.0 (17.0, 21.6) B
Kruskal-Wallis <i>H</i>	60.98	52.4	34.49
<i>p</i>	<0.0001	<0.0001	<0.0001

Table 3: Comparisons of the opening sizes gnawed in black walnut shells by one adult female and two juvenile red squirrels to access and remove nutmeats. Values are medians with 25th and 75th percentiles in parentheses. Sample sizes are 440, 24, and 62 for values in columns 2 and 3 and 220, 12, and 31 for column 4 for the three different squirrels, respectively. Results of Kruskal-Wallis tests are shown separately for each variable. Within each column, values not having a letter in common are significantly different from one another (Tukey's LSD tests).

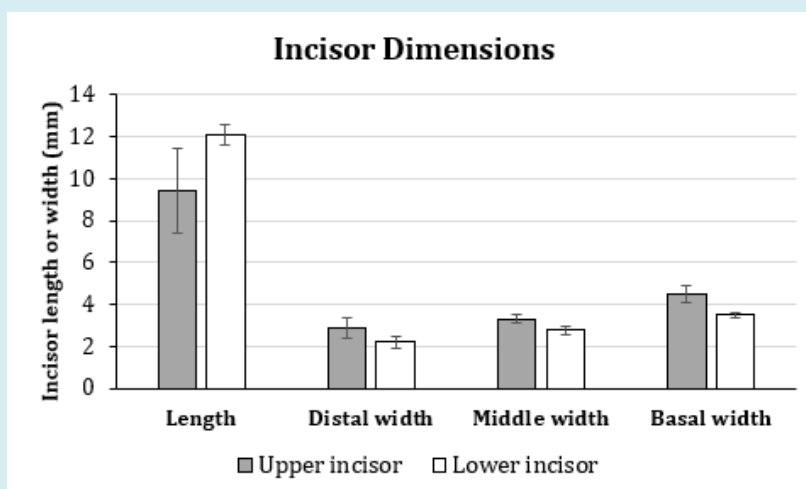


Figure 3: Mean ($\pm$ one standard deviation) dimensions of American red squirrel incisors measured from four intact skulls in Winona, Minnesota USA museum collections. Widths are for both incisors combined.

Red squirrel incisors dimensions displayed consistent patterns across the four skulls (of unknown age) measured. Lower incisors averaged 29% longer than the upper incisors, whereas upper incisors had combined widths 18 to 32% greater than those of the lowers (Figure 3). Combined widths increased 1.5 to 1.6-fold between distal and basal ends. The dimensions of the openings created by red squirrels in walnut shells were roughly six to seven times the widths of the distal incisors.

Discussion

Examination of black walnuts, both uneaten shells and those eaten by adult and juvenile American red squirrels, revealed two main findings about walnut handling by red squirrels. First, both adult and juvenile squirrels selected nuts to eat that were significantly wider (but not longer) than those that were not eaten, but selectivity did not differ among an adult and two juvenile squirrels. Second, an adult female red squirrel created significantly smaller openings to access and remove all walnut nutmeats from shells compared to those needed by two juvenile red squirrels to accomplish complete nutmeat extraction.

Throughout their geographic range across northern, eastern, and mountainous western North America, the American red squirrel consumes a variety of foods, including conifer seeds, nuts, berries, leaf buds, fungi, and several animal-based foods such as bird eggs and insect larvae [1-7,22-24]. Conifer seeds often dominate red squirrel diets in northern forests, with nuts becoming more common diet items in deciduous forests [1-7,22-24]. Versatile sharp incisors can easily extract conifer seeds from woody cones and successfully extract nutmeats from a variety of hard nut shells [3]. Although not typically comprising a large portion of red, gray, or fox squirrel diets [2,7,17], black walnuts are eaten regularly during fall and winter seasons wherever and whenever they are abundantly available in portions of the approximately 18 USA states where red squirrel and black walnut ranges overlap [3,7,10,11]. Black walnuts and other native nuts provide squirrels with a high-nutrient food resource [15]. Nuts can vary significantly in their accessibility to feeding squirrels, some having thin shells and others, like black walnuts, armored in thick, highly protective shells [12,15]. Difficulty accessing the well-protected nutmeats likely prevents squirrels from maximizing their rates of food intake [9,25].

To maximize feeding efficiencies, tree squirrels may initially select black walnuts based on some tactile assessment of size or quality. Fox squirrels have been observed manipulating nuts in their paws and mouths, assessing nut size or weight before eating or rejecting individual nuts [13]. Size selectivity should be important to foraging squirrels, as

small nuts may provide little nutritional reward for the effort and large nuts may pose severe handling problems [9]. Both adult and juvenile red squirrels in my study consumed black walnuts that were significantly wider than the nuts generally available in the environment for eating, suggesting some degree of selection for the larger nuts that likely contained larger nutmeats. Whether this selection is a learned or innate behavior cannot be determined from my study. Although the selection of larger nuts by both juveniles and an adult might suggest it being innate, previous studies have reported that young (6-month-old) tree squirrels (including red squirrels) are able to quickly learn optimal feeding techniques for use on thick-shelled nuts [8,21].

Tree squirrels expend a significant amount of time accessing the nutmeats contained within nut shells. While some types of nuts can be extracted from their shells in 1 to 6 minutes [18,19,26], others may require 25 to 75 minutes per nut [8]. My single observation of an adult female squirrel that required nearly 8 minutes to process and consume a single walnut falls within the range of these previous observations. Given the amount of time needed for red squirrels to remove nutmeats from a walnut shell, any extraction method that can shorten the time required would allow squirrels to increase food consumption rates and/or reduce the energetic costs of feeding [8]. By extracting the entire nutmeat contained within a shell through smaller gnawed openings, the adult female red squirrel in our study likely spent less time feeding on each walnut compared to her juvenile offspring and probably had a higher rate of food intake. Because she appeared to be more efficient when feeding on black walnuts compared to her offspring, she also may have been more willing than the juveniles to make walnuts a dominant portion of her diet. The large number (220) of predated walnut shells in the adult female's midden compared to much smaller numbers (12 and 31) in the juveniles' middens seem to suggest that the juveniles were consuming other foods in addition to black walnuts. Alternatively, juveniles also had to contend with their mother's defense of her walnut cache around the black walnut tree, probably being forced into pilfering walnuts from their mother's cache [4-6,24] if the opportunity arose, limiting the numbers of black walnuts available to them (and possibly slowing their learning process of feeding on walnuts).

Older tree squirrels usually are more experienced than their offspring at accessing and handling various food items, allowing them to maximize their food intake [8,9,19]. The fact that juvenile red squirrels in the present study created significantly larger openings in shells than an adult squirrel to feed on the nutmeat was not unexpected, as using the best approach to access and extract the contents from a thick and hard shell likely requires some period of learning [8]. How long this learning might take is not known, although

juvenile red squirrels in a previous study exhibited improved nut handling times over periods up to 12 weeks after first exposure [8]. In the present study, one of the two juveniles appeared to be creating smaller openings in walnut shells than its sibling, and those openings were of the same relative size (based on percent of total nut area) as those made by its mother. Although walnuts eaten by red squirrels were not monitored after November, I suspect that with continued exposure to black walnuts, both juveniles likely became more skilled at feeding on walnuts and could do so through smaller gnawed openings while walnuts were still available into the winter months.

Conclusions

Both adult and juvenile red squirrels select and feed on black walnuts that are wider on average than those available, and they extract the nutmeat by gnawing only two holes in opposite sides of the shell. Adult squirrels gnaw significantly smaller openings than juveniles to get at the nutmeat, suggesting that juveniles need a period of learning to become more proficient at feeding on black walnuts.

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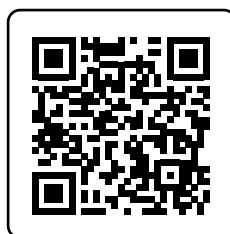
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