

The anatomy of a range expansion: changes in cranial morphology and rates of energy extraction for North American red squirrels from different latitudes

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Species with expanding ranges provide unique opportunities to examine environmentally induced adaptations in ecological traits and anatomical characteristics. Since the late 1800s, the North American red squirrel (*Tamiasciurus hudsonicus*) has expanded its range into the central hardwoods of the United States in conjunction with increasing agricultural fragmentation. We examined whether red squirrels from the central hardwoods (west-central Indiana, USA) displayed differences in foraging behaviors and morphology relative to red squirrels from conifer-dominated environments (upper peninsula of Michigan, USA), a biome in which red squirrels evolved. Specifically, we measured rates of energy extraction, variation in cranial morphology, and diet preference between red squirrels from both regions. In addition, we compared foraging behaviors of red squirrels from the central hardwoods to those of a competitor that coevolved with nut-producing trees, the gray squirrel (*Sciurus carolinensis*). Red squirrels from Indiana and Michigan differed significantly in the efficiency with which they used food items, with individuals from each region extracting calories at a more rapid rate for items that were common in their region. The enhanced efficiency of southern red squirrels feeding on black walnuts (*Juglans nigra*) was correlated with geographic differences in cranial morphology; skulls of southern squirrels were larger, with longer jaws and higher metrics associated with greater mandibular force than northern squirrels. Contrary to our expectations, red squirrels from Indiana and Michigan did not differ qualitatively in preferences for food items, suggesting that diet choice may be governed by perishability of food items rather than by rates of energy extraction. Gray squirrels were more efficient than Indiana red squirrels in using all food items, and differed only slightly from red squirrels with regard to preference for food items. Measures of efficiency of resource use, after accounting for species-specific metabolic requirements, suggest that red squirrels are unlikely to compensate ecologically for declining gray squirrel populations in fragmented portions of the central hardwoods, with potentially adverse effects for forest regeneration and succession. Our results demonstrate that invading species can display significant flexibility in adapting to new environments, but they may not be flexible enough to exploit resources in a manner comparable to native species.

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Geographic range size is a property emerging from many facets of a species' biology, including body size, abundance, and, in particular, niche breadth (Brown 1995). Range boundaries fluctuate in response to altered biotic or abiotic conditions (Dark et al. 1998, Pilson 1999, Hellberg et al. 2001), and the extent to

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which a species can broaden its niche is of vital importance in determining whether and to what extent that species can invade new environments (Thomas et al. 2001). Flexibility in behavioral, morphological, or physiological characteristics of a species may facilitate exploitation of previously unused or unavailable resources, thus resulting in range expansion of that species.

Ecological flexibility may arise as a result of different processes. In phenotypically plastic species, multiple phenotypes may arise from a single genotype in response to environmental pressures (West-Eberhard 1989, de Jong 1995). Selection also may occur such that genotypes are modified to promote local adaptation and thus persistence of a species in a previously unoccupied area or region (Wiernasz 1989, Alisauskas 1998, Thomas et al. 2001).

Invariant requirements of a species may necessitate behavioral or ecological flexibility in meeting other, less critical requirements. For example, pronghorn (*Antilocapra americana*) are selective browsers throughout the majority of the year (O'Gara 1978) and, consequently, mating system and group size vary in the species with distribution of dietary resources (Maher 1994, see also Komers 1997). Thus flexibility in a biological trait such as social structure in pronghorn may reflect adaptive or compensatory responses to environmental variability such that other, less flexible traits, e.g. resource selection, remain unaltered.

The North American red squirrel (*Tamiasciurus hudsonicus*; hereafter red squirrel) is a relatively recent colonist of the central hardwoods region of the midwestern United States. Range expansion of red squirrels is ongoing (Swihart et al., unpubl.) and probably has been facilitated by a reduction in numbers of more fragmentation-sensitive competitors, specifically gray squirrels (*Sciurus carolinensis*). Gray squirrels in the midwestern United States have been affected negatively by agriculturally induced fragmentation of forest (Nixon et al. 1978, Nupp and Swihart 2000) and, at our study sites, share a high degree of resource overlap with red squirrels (Ivan and Swihart 2000). Further, Nupp and Swihart (2001) detected significant competitive effects between red and gray squirrels based on density estimates from trapping data (but see Ackerman and Weigl 1970, Riege 1991).

Given this relatively recent range expansion, we were interested in whether red squirrels from Indiana had broadened their dietary niche relative to ancestral populations. Specifically, we compared the degree to which foraging behaviors of red squirrels from a predominantly deciduous environment in the central hardwoods region differed from those from a predominantly coniferous environment. Specifically, we tested whether red squirrels exhibited flexibility between regions with regard to: 1) the rate at which individuals extracted energy from food items of varying characteristics and

familiarities; and 2) preferences of individuals for these food items. We hypothesized that resource-use efficiency, indexed by rates of energy extraction, would be greater for familiar food items. Accordingly, we predicted that extraction rates for food items native to the central hardwoods (acorns, walnuts) would be significantly less for Michigan red squirrels than for Indiana red squirrels. Similarly, we predicted that extraction rates for food items native to northern forests (conifer cones) would be significantly less for Indiana red squirrels than for Michigan red squirrels.

Differences in the energy extraction rates between red squirrels from different regions would provide preliminary evidence that red squirrels have broadened their niche in conjunction with or as a consequence of range expansion. To investigate a potential mechanism responsible for this niche expansion, we collected data on cranial size for red squirrels from Indiana and the upper peninsula of Michigan in an effort to evaluate differences in morphological characteristics associated with feeding. A failure to detect differences in cranial morphology would imply that range expansion has occurred independently of environmental selection on cranial morphology, such that any differences in efficiency of resource use could be attributed to differential behaviors stemming from phenotypic plasticity or learning (*sensu* Weigl and Hanson 1980). Alternatively, if differences in cranial morphology related to the processing of food items were observed, the importance of environmental selection in facilitating range expansion would be supported. In a recent study, Beldade et al. (2002) demonstrated that natural selection can play a more dominant role than internal developmental constraints in shaping existing variation in species.

Additionally, we hypothesized that preference for a food item would reflect previous exposure to and experience with the food item. Thus, we predicted that Michigan red squirrels would preferentially select conifer cones over nuts, and Indiana red squirrels would preferentially select nuts over conifer cones (see "previous exposure hypothesis", Table 1). Alternatively, red squirrels could select food items innately based on the amount of energy extracted per unit time (see "efficiency of energy extraction hypothesis", Table 1; Smith and Follmer 1972) or the elapsed time to germination after the production of fruit (see "perishability hypothesis", Table 1; Post and Reichman 1991, Hadj-Chikh et al. 1996). We focused our attention on seeds with varying levels of perishability. Unmanipulated black walnuts (*Juglans nigra*) can be viable for up to 4 years (Young and Young 1992), and thus represent the least perishable species used in our handling-time and resource preference trials (Table 1; see below). Bur oak acorns (*Quercus macrocarpa*) are in the white oak group (subgenus *Leucobalanus*), and thus germinate 1 year prior to red oak (*Q. rubrum*) acorns in the red oak group (subgenus *Erythrobalanus*). White spruce (*Picea*

Table 1. Predicted strength of preferences for food items by Indiana and Michigan red squirrels under 3 different scenarios. Under the “previous exposure” hypothesis, preferences should be greatest for food items common to the region occupied by the study animals. The “efficiency of energy extraction” hypothesis predicts that preferences will covary with the rate at which calories are extracted from food items, as given in Fig. 1. Under the “perishability” hypothesis, food items that are low in perishability should be preferred. Note here that preference is measured by selection of a food item, not by immediate consumption; items of low perishability often are selectively hoarded by squirrels, whereas items of lower preference are subsequently selected and consumed immediately. Two sets of predictions are given under the “perishability” hypothesis for Michigan squirrels, based on whether individuals actively manage cache sites. No evidence of cache management exists for Indiana red squirrels (see text).

Previous exposure	
Indiana red squirrel	black walnut = bur oak = red oak > white spruce
Michigan red squirrel	white spruce > black walnut = bur oak = red oak
Efficiency of energy extraction	
Indiana red squirrel	red oak = bur oak ≥ white spruce > black walnut
Michigan red squirrel	white spruce > red oak = bur oak > black walnut
Perishability ^a	
Indiana red squirrel	black walnut > red oak > bur oak > white spruce
Michigan red squirrel	
unmanaged	black walnut > red oak > bur oak > white spruce
managed	black walnut > white spruce > red oak > bur oak

^a from Young and Young (1992).

glauca) seeds disperse in autumn (Young and Young 1992), and thus represent the most perishable species used in our handling-time and resource preference trials (Table 1; see below). Although red squirrels do not typically consume conifer seeds that have dispersed, red squirrels from northern latitudes manipulate perishability of conifer seeds by storing seed-filled cones in middens. Temperature and humidity in middens prevent cones from opening, thereby prolonging the viability of seeds (Smith 1968, 1981). However, red squirrels in eastern North America commonly scatterhoard and do not actively manage perishability of items in these hoards (Layne 1954, Dempsey and Keppie 1993). If red squirrels do not differ between regions in their efficiency of use of food items or in their resource preferences, behavioral rigidity highlights the importance of these behaviors throughout the species' range.

The functional role (i.e. the way in which organisms interact with each other and with their environment, Huston 1994) of scatterhoarding squirrels is important in forest regeneration processes, and coevolutionary ties existing between mast-producing trees and scatterhoarding squirrels are at least partially responsible for forest succession (Stapanian and Smith 1978, Steele et al. 1993, Vander Wall 1990, 2001). Red squirrels may not be functionally analogous to gray squirrels if they differ from gray squirrels in their efficiency of hard mast use or food preferences. Thus, the extent to which red squirrels in the midwestern United States can broaden their niche to fill the functional role held by gray squirrels (sensu the “redundancy hypothesis”; Walker 1992) has ramifications for forest regeneration and successional dynamics.

We also compared Indiana red squirrels and gray squirrels with regard to efficiency of use of different food items and food preferences. Given that gray squirrels are approximately twice as large as red squirrels

and have coevolved with nut-producing trees, we expected gray squirrels to be more efficient in processing different species of hard mast. Regardless of whether red squirrels are actively displacing gray squirrels, range expansion of red squirrels in conjunction with declining gray squirrel populations has important implications for the structure and function of granivore and forest communities of the central hardwoods.

Materials and methods

Study site

To test our hypotheses of resource-use efficiency and preference, we observed red squirrels in two regions characterized by vastly different biotic communities. The study site for behavioral observations in the central hardwoods was a 2.5 ha forest fragment associated with a horticultural park in Tippecanoe County in west-central Indiana. This area approximates the southern periphery of the range of the red squirrel in the midwestern United States (Mumford and Whitaker 1982). Squirrels used in handling-time trials were captured at other forest fragments in Tippecanoe County. Dominant tree species at both observational and trapping sites included oaks (*Quercus* spp.), hickories (*Carya* spp.), maples (*Acer* spp.), and black walnut. Conifers were present but uncommon at both observational and trapping sites.

The study site for behavioral observations in the boreal forest was located within ca 1330 ha of privately owned contiguous forest in Iron County in the southwestern upper peninsula of Michigan. Squirrels used in handling-time trials were captured at other sites in the Ottawa National Forest > 30 km from the observational site. Thus, individuals used in handling-time

trials were different from those observed in the field. Gray squirrels were not notably abundant at either observational or trapping sites in Michigan. Dominant tree species at both observational and trapping sites included white spruce, red pine (*Pinus resinosa*), eastern hemlock (*Tsuga canadensis*), quaking aspen (*Populus tremuloides*), and sugar maple (*Acer saccharum*). Although northern red oak and bur oak are present in the Michigan upper peninsula, they are rare and were absent at the observational and trapping sites. Moreover, bur oak likely did not occur in the upper peninsula before European settlement (Harlow and Harrar 1969). Black walnut is not native to the Michigan upper peninsula (Harlow and Harrar 1969).

Handling-time trials

Handling-time trials were conducted from 16 April to 1 August 2001 to provide measures of efficiency of use for 3 species of mast common to the central hardwoods and known to be important components of red and gray squirrel diets (Korschgen 1981, Steele 1998): northern red oak, bur oak, and black walnut. In addition, we measured efficiency of use of white spruce cones for red squirrels in both Indiana and Michigan. Red squirrels typically are regarded as conifer specialists (Smith 1968, Steele 1998), and white spruce is a common component of red squirrel diets throughout the majority of the species' historic range. Only adult male and adult non-pregnant, non-lactating female individuals were used in the experiment. Walnuts and acorns used in the trials were purchased from commercial vendors (F. W. Schumacher Company and Sheffield's Seed Company, New York). We collected spruce cones from Indiana and Michigan, and cones from both sites were mixed in presentations. All food items were refrigerated until use. We discarded acorns that were noticeably rotten and discarded spruce cones that had opened. During trials, black walnut was presented without husks and acorns were presented without pericaps.

Squirrels used in handling-time trials were captured in Tomahawk™ live traps baited with English walnuts or pecans and a peanut butter/oat mixture. Squirrels were maintained individually in holding pens (61.0 × 40.6 × 35.6 cm) constructed of stainless steel and hardware cloth. Each pen contained a wooden nest box with the top panel removed to facilitate monitoring of individuals. Squirrels were maintained at a constant temperature (21°C ± 3°) and a 12L:12D photoperiod. A sunflower seed/corn mixture and water were provided ad lib before handling-time trials. All test subjects were held for 1–2 days before trials to ensure that squirrels were eating and had acclimated to captivity.

Squirrels were monitored 8–10 h/day between 0700 and 1700 h. Squirrels were monitored continuously

using Sony® hand-held video camera recorders with 8 mm video tapes. Because tape duration was limited, we exchanged tapes 2 times a day at 4 h intervals. Cameras were affixed to tripods and were positioned approximately 1 m above holding pens.

One item of 1 food type was presented to individual squirrels at a given time. Food items were weighed to the nearest 0.001 g before presentation. Each squirrel was presented with each food type, with the exception of gray squirrels and white spruce cones. Order of presentation was determined randomly. A food item was presented for the 8–10 h/day that squirrels were monitored. After this time, food items that were not consumed were removed and replaced with sunflower seed/corn mixture. Following consumption of a food item, we removed the remains of the food item from the pen and the catch tray underneath the pen. Care was taken to ensure that all uneaten fragments were collected. Uneaten fragments were weighed following collection. Food items were presented for a maximum of 2 days. If a food type was untouched following this time period, it was not presented again.

Following monitoring events, we recorded handling times by viewing tapes associated with individuals processing different food items. We defined handling time as the time required to consume an item (sensu Stephens and Krebs 1986). All activities noted in the processing of an item (gnawing, chewing, rolling of food items, etc.) were used in measuring handling time. We then calculated a metric of efficiency of use: $(W_o - W_f)/T$ where W_o , W_f , and T are the original mass of the food item (g), the mass of the fragments (g) following consumption, and handling time (min), respectively.

Cranial morphology

To investigate morphological mechanisms causing differences in efficiency of resource use, we measured 7 cranial characters of Indiana and Michigan red squirrels. These characters were selected on the basis of biological relevance (Ball and Roth 1996, Thorington and Darrow 1996, Velhagen and Roth 1997) and provided estimates of functionally relevant mandibular characters, jaw elongation, and skull size. Specifically, we measured the moment arm of the deep masseter muscle (MDM), the moment arm of the temporalis muscle (MT), and the moment arm of the superficial masseter (MSM) for metrics of mandibular force (measurements taken as described by Thorington and Darrow 1996 and Velhagen and Roth 1997); the middle of the mandibular condyle to the anterior edge of the P3 alveolus (DP4) and the middle of the mandibular condyle to the posteroventral edge of the lower incisor alveolus (JL) for metrics of jaw elongation; and the posterior margin of the occipital bone to the posterior margin of the upper incisor alveolus (SL) and the

distance across the lateral-most margins of the zygomatic arches (SW) for metrics of skull size.

Specimens with fully erupted adult dentitions were measured to the nearest 0.01 mm using Mitutoyo digital calipers. Specimens were measured at the Field Museum, Indiana State University, Oklahoma State Museum of Natural History, Purdue University, University of Illinois, and University of Michigan. All measurements were taken by JHR. In addition to collecting skull measurements, collection date and total and tail lengths were recorded from each specimen's museum tag when available. Head and body lengths were calculated by subtracting tail length from total length. This indicator of body size is preferable to total length because some tail lengths were recorded to the tip of the hair and some to the last vertebrae.

Resource preferences

Field trials to assess resource preferences were conducted 6 June to 29 June 2000 and 31 May to 27 June 2001. The timing of our field trials corresponds with the period in which spruce cones are first consumed in significant amounts by red squirrels in mixed coniferous forests (Ferron et al. 1986). Feeding stations were constructed by gluing 4 square petri dishes on a 50 × 10 cm piece of plywood, with 3 to 4 items of each food type (including white spruce) in different petri dishes. Petri dishes were spaced about 3 cm apart. Stations were placed in 12 locations in both Indiana and Michigan. Stations were spaced ≥ 200 m apart in Indiana and 300 m apart in Michigan, making it highly unlikely that multiple stations were visited by an individual (Layne 1954, Riege 1976, Rusch and Reeder 1978, Goheen and Swihart, unpubl.). Further, observers often were able to identify individual squirrels and thus make sure individuals were not visiting multiple stations.

Data on resource preference were recorded by observers hidden approximately 30 m from feeding stations between 0600 and 1100 h. In addition to recording the number, type, and order of food items taken, observers in Indiana recorded the fate of each food item (eaten, scatterhoarded, larderhoarded). Dense understory obstructed vision in Michigan, preventing fates of most food items from being recorded. A station was monitored until a trial had been recorded by 1 red squirrel and 1 gray squirrel in Indiana or 1 red squirrel in Michigan, with the criterion that each individual was offered the full complement of resources from which to choose. Occasionally, eastern chipmunks (*Tamias striatus*) would visit stations and consume food items in the middle of a trial. These trials were omitted from analyses.

We determined resource preference for each food type and squirrel group (Indiana red squirrels, Michigan red squirrels, and Indiana gray squirrels) based on

the number, type, and order of food items taken in a foraging bout. We defined the length of a foraging bout as the time elapsed between the 1st and last feeding events at a particular station. Foraging bouts averaged 15.04 min ± 9.19 SD for trials, and < 3 min usually elapsed between visits by an individual.

Statistical analyses

We compared efficiency of use for red oak acorns, bur oak acorns, and black walnuts across squirrel groups using 1-way ANOVA. A posteriori multiple pairwise comparisons (LSD method) were used to test efficiency of use between red squirrels from the 2 latitudes and between red and gray squirrels. We used an independent samples 2-tailed *t*-test to compare efficiency of use for white spruce cones between red squirrels from Indiana and red squirrels from Michigan.

All 7 cranial variables were natural log transformed prior to analyses. We divided data into 4 groups based on sex and locality. Discriminant analysis was used to assign 6 individuals of unknown sex to appropriate groups within each location. Following Storz et al. (2001), we used 2-way MANOVA to evaluate differences in squirrels based on location, sex, and a sex × location interaction. Variance-covariance matrices from each group were compared using the jump-up approach to Flury's hierarchy of matrix comparisons (Phillips and Arnold 1999). This approach provides a test of the MANOVA assumption of equality of variance-covariance matrices and suggests an appropriate matrix model for subsequent principal components analysis (PCA).

We utilized the first axis from the PCA of the 7 cranial variables to derive a multivariate measure of cranial size. Similarities in the relationship between head size (PCI scores) and year of collection were evaluated via simple linear regression and ANCOVA for both Indiana and Michigan red squirrels. Data from the late 1800s and early 1900s was excluded from the Michigan sample to provide better overlap between the ranges of collection times for squirrels from both regions.

We calculated selection ratios (w ; Manly et al. 1993) for each food type on n individuals within a group ($j = 1, \dots, n$) as $w_i = u_{i+} / \sum(\pi_{ij}u_{+j})$, where u_{i+} is the total number of items of food type i consumed by all n individuals within a group, π_{ij} is the proportion of food items of type i available to individual j , and u_{+j} is the total number of all items consumed by individual j . Preference, avoidance, and no selection of a food type i are given by $w_i > 1$, $w_i < 1$, and $w_i = 1$, respectively. We computed simultaneous Bonferroni confidence intervals to test for significant deviations of w from 1.0.

Proportional hazards models were developed to predict use of food types over time using RSF software

(version 1.02A, Manly 1993). Models were fitted by the method of maximum likelihood and estimated the probability of use, P , for a given seed type, X , after a specified time, t , as $P = 1 - \exp\{-[\exp(b_0 + b_1X_1 + \dots + b_pX_p)]t\}$. Seed types were represented by a series of 3 dummy variables in the analyses.

To standardize between trials of unequal length, we divided each trial into 4 intervals based on the proportion of time elapsed within that particular trial: 0–25%, 25–50%, 50–75%, and 75–100% (Ivan and Swihart 2000). Thus, data were treated as the number of items of a particular food type taken during the first quarter of the trials, during the second quarter of the trials, etc. In all trials, number of seeds of each type remaining after a trial had ended was tallied and used in the proportional hazards model.

Observational data on fates of food items were analyzed using Chi-square analyses. Gray squirrels typically buried food items that were not consumed immediately in single caches (i.e. scatterhoarding), whereas red squirrels often larderhoarded food items or hoarded food items in trees. Observational data regarding fates of food items were pooled into 2 categories, hoarded or eaten. This provided an additional test of hypotheses relative to characteristics of food types and their influence upon selection, since food items that are consumed immediately generally are more perishable relative to those that are hoarded (Smith and Reichman 1984, Gendron and Reichman 1995, Hadj-Chikh et al. 1996).

Results

Handling-time trials

We offered 1 red oak acorn, 1 bur oak acorn, 1 black walnut, and 1 white spruce cone to each of 14 Indiana red squirrels and 14 Michigan red squirrels. We offered 1 red oak acorn, 1 bur oak acorn, and 1 black walnut to each of 14 gray squirrels in Indiana. Of the Indiana red squirrels, 2 did not attempt to consume black walnuts, 2 did not attempt to consume white spruce cones, and 1 did not attempt to consume a bur oak acorn. Of the Michigan red squirrels, 1 did not attempt to consume a black walnut. Of the gray squirrels, 2 did not attempt to consume black walnuts.

Squirrels from each group differed in their efficiency of use for black walnut ($F = 56.98$, $d.f. = 2, 36$, $P < 0.001$), red oak acorns ($F = 18.86$, $d.f. = 2, 41$, $P < 0.001$), and bur oak acorns ($F = 29.20$, $d.f. = 2, 39$, $P < 0.001$). Consistent with our hypotheses, Indiana red squirrels were more efficient at consuming black walnut ($P < 0.001$) and bur oak acorns ($P = 0.04$) than Michigan red squirrels (Fig. 1). Michigan red squirrels were more efficient consumers of white spruce cones than Indiana red squirrels ($t = 4.32$, $d.f. = 24$, $P = 0.007$; Fig.

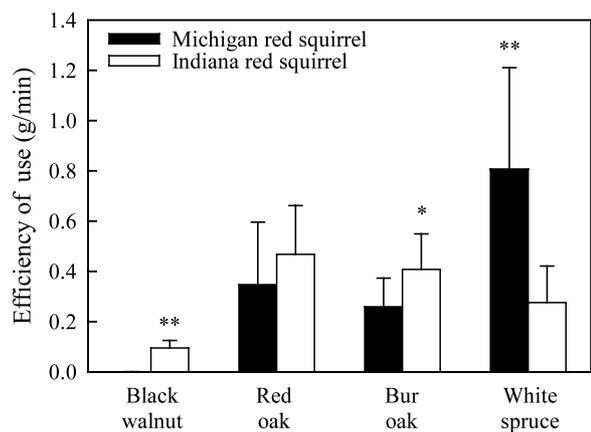


Fig. 1. Rates of energy extraction for Indiana red squirrels and Michigan red squirrels with 4 types of food items. One asterisk above error bars represents significant differences between squirrels from the two localities at $P < 0.05$; 2 asterisks above error bars represents significance at $P < 0.01$.

1). Gray squirrels were more efficient consumers of black walnut ($P < 0.001$), red oak acorns ($P < 0.001$), and bur oak acorns ($P < 0.001$) than Indiana red squirrels (Fig. 2).

Cranial morphology

Variables MSM in female Michigan red squirrels and MDM in female Indiana red squirrels departed significantly from univariate normality (Shapiro-Wilks $P < 0.05$). However, multivariate non-normality was not apparent upon examination of principal components ordinations, and variance-covariance matrices were homogeneous across groups ($\chi^2 = 89.151$, $d.f. = 84$, $P > 0.30$).

Two-factor MANOVA (Table 2) revealed significantly different cranial measurements as a function of

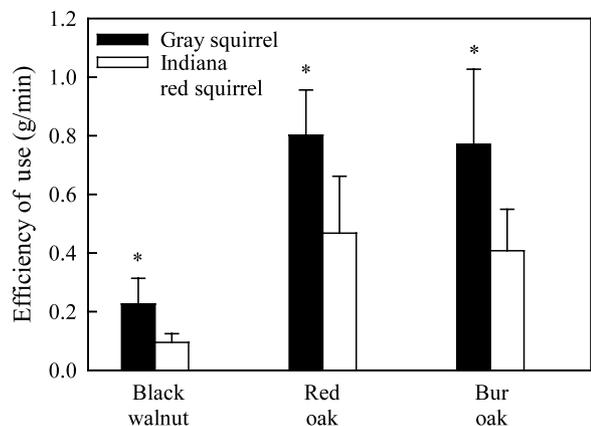


Fig. 2. Rates of energy extraction for Indiana red squirrels and gray squirrels with 3 types of food items. Asterisks represent significance at $P < 0.001$.

Table 2. Results of a two factor MANOVA to evaluate differences in the crania of Indiana and Michigan red squirrels.

Source	<i>d.f.</i>	Pillai's trace	<i>F</i>	<i>P</i>
Location	7, 124	0.3215	8.3946	<0.0002
Sex	7, 124	0.0627	1.1851	0.3162
Location × Sex	7, 124	0.0232	0.4224	0.8868

geographic locale ($F = 8.39$, $d.f. = 7, 124$, $P < 0.001$). No significant differences were detected as a function of sex ($F = 1.19$, $d.f. = 7, 124$, $P > 0.30$) or sex × locale interaction ($F = 0.42$, $d.f. = 7, 124$, $P > 0.85$). *F*-tests indicated that means were significantly larger ($P < 0.001$) for Indiana red squirrels across all 7 cranial characters.

Homogeneity of variance-covariance matrices indicated that the data met assumptions of Thorpe's multiple group principal components analysis (MGPCA; Thorpe 1988 and references therein). Accordingly, PCs and PC scores were computed from a variance-covariance matrix pooled between groups. Uniform signs and a large eigenvalue for MGPC1 indicated the axis represented head size. The majority of cranial variation in our sample was due to shape consequences of size change, or allometry. Comparison of MGPC1 eigenvector coefficients (Table 3) with an isometry value, 0.38 indicates the nature of each character's allometric variation in relation to overall cranial size. The isometry value is calculated as $(1/p)^{0.5}$ where *p* equals the number of characters (Klingenberg 1996). Coefficients greater than 0.38 indicate positive allometry, smaller coefficients indicate negative allometry, and coefficients approximately equal indicate isometry.

Analysis of covariance interaction terms were not significant, indicating that slopes were homogeneous ($F = 0.80$, $d.f. = 1, P > 0.35$) between year and cranial size (Fig. 3). Intercepts differed significantly ($F = 29.93$, $d.f. = 1, P < 0.001$), reiterating the cranial size differences revealed by MANOVA. Additionally, ANCOVA results indicated slopes were homogeneous ($F = 0.11$, $d.f. = 1, P > 0.70$) in the relationships between time and

Table 3. Characteristics of the first principal component from the MGPCA used to represent head size of North American red squirrels. Coefficients > 0.38 indicate positive allometry, whereas coefficients < 0.38 indicate negative allometry (see text for details).

Character	MGPC1
MDM	0.3695
MT	0.4394
MSM	0.4967
DP4	0.3554
JL	0.3550
SL	0.2623
SW	0.3202
Eigenvalue	0.0073
Variation accounted for (%)	78.79

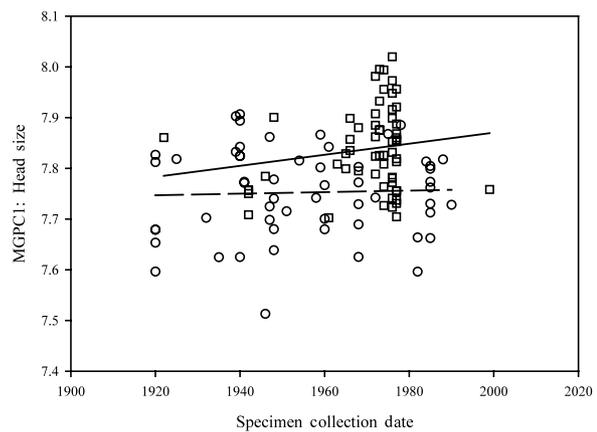


Fig. 3. The relationships between head size and year of collection for Indiana (squares and solid line, $y = 5.68 + 0.0011x$, $r^2 = 0.027$, $P = 0.2092$) and Michigan (circles and dashed line, $y = 7.44 + 0.0001x$, $r^2 = 0.002$) red squirrels.

body size (Fig. 4). Again, intercepts differed significantly ($F = 6.92$, $d.f. = 1, P = 0.01$), revealing a significant difference in body size between Indiana and Michigan red squirrels.

Resource preferences

Calculation of selection ratios revealed patterns of selection across groups of squirrels. White spruce consistently was avoided across groups, whereas bur oak was selectively neutral across groups (Table 4). Indiana red squirrels selected black walnut relative to other food items, whereas Michigan red squirrels selected black walnut and red oak acorns (Table 4). Gray squirrels selected red oak acorns relative to other food items (Table 4).

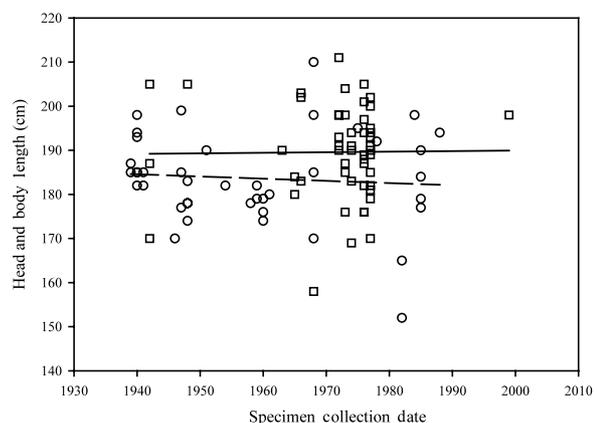


Fig. 4. The relationships between body size and year of collection for Indiana (squares and solid line, $y = 164.18 + 0.0129x$, $r^2 = 0.0001$, $P = 0.9353$) and Michigan (circles and dashed line, $y = 281.80 - 0.0501x$, $r^2 = 0.006$) red squirrels.

Table 4. Resource selection ratios computed for squirrel groups offered 4 types of food items in field trials. Selection ratios represent results pooled across individuals within a group. Values of w followed by an asterisk were different from 1.0 ($P < 0.05$), where $w < 1$ indicates avoidance and $w > 1$ indicates preference. Numbers in parentheses represent standard errors (Manly et al. 1993).

Food item type	Indiana red squirrel ($n = 12$)	Michigan red squirrel ($n = 13$)	Gray squirrel ($n = 13$)
Black walnut	1.60* (0.14)	1.26* (0.06)	1.15 (0.13)
Red oak	1.22 (0.12)	1.18* (0.04)	1.57* (0.09)
Bur oak	1.02 (0.12)	1.01 (0.06)	1.24 (0.12)
White spruce	0.18* (0.11)	0.34* (0.08)	0.04* (0.04)

Individuals from each squirrel group took at least 1 item of all food types on at least 1 occasion, although white spruce cones were taken infrequently by gray squirrels and Indiana red squirrels (gray squirrels: 1 recorded observation out of 104 items taken, Indiana red squirrels: 4 recorded observations out of 84 items taken). Because of this, we developed a second set of proportional hazards models for these groups that excluded white spruce.

Proportional hazards models of selection including all 4 food types provided significant improvements in fit relative to null models of no selection ($P < 0.001$ for all tests). Hazard models including all food types appeared to provide a good fit for gray squirrel data ($\chi^2 = 7.07$, $d.f. = 9$, $P > 0.50$), but a poor fit and a moderate fit for Indiana red squirrel ($\chi^2 = 27.94$, $d.f. = 12$, $P < 0.01$) and Michigan red squirrel ($\chi^2 = 18.58$, $d.f. = 9$, $P < 0.08$) data, respectively. Hazard models of selection excluding white spruce provided significant improvements in fit relative to null models of no selection for Indiana red squirrel ($P < 0.001$) and gray squirrel ($P < 0.01$) data. Hazard models excluding white spruce appeared to provide a better fit for Indiana red squirrel ($\chi^2 = 8.96$, $d.f. = 6$, $P > 0.15$) and gray squirrel ($\chi^2 = 5.18$, $d.f. = 6$, $P > 0.50$) data. Nuts were taken preferentially to cones by Michigan red squirrels, and Indiana red squirrels removed walnuts preferentially relative to acorns (Fig. 5). Gray squirrels removed red oak acorns preferentially to bur oak acorns and walnuts (Fig. 5).

Red oak acorns and black walnuts were hoarded significantly more often than they were eaten by Indiana red squirrels and gray squirrels ($d.f. = 1$, $P < 0.003$ for all tests). Bur oak acorns were eaten and hoarded according to null expectation for both squirrel groups (Indiana red squirrels: $d.f. = 1$, $P = 0.49$; gray squirrels $d.f. = 1$, $P = 0.45$).

Discussion

We observed striking differences in rates of energy extraction between red squirrels from hardwood-dominated environments and those from a mixed-coniferous forest. The efficiency of use of black walnuts by Indiana red squirrels was several orders of magni-

tude greater than that of Michigan red squirrels; similarly, the efficiency of use of bur oak acorns by Indiana red squirrels was significantly greater than that of Michigan red squirrels. Our results concur with other studies demonstrating the impact of habitat upon one or more components of foraging efficiency (Werner and Hall 1979, Mittelbach 1981, Day and McPhail 1996).

Differences in the efficiency of use of black walnut and bur oak acorns, coupled with differences in cranial morphology between Michigan and Indiana red squirrels, support the implied relationship between the properties of food items and jaw structure. Smith (1970) studied *Tamiasciurus* species in the Pacific Northwest region of North America. He observed that squirrels that ate harder serotinous pine cones had more robust crania than squirrels eating softer, non-serotinous pine cones. Weigl et al. (1998) analyzed morphological features of fox squirrels (*Sciurus niger*) and noted that, unlike several other cranial characters, characters associated with feeding did not vary clinally with climatic variables in the central hardwoods region. Similarly, Barnett (1977) failed to find variation in the majority of measured functionally relevant mandibular characters of gray squirrels across latitudes. In contrast, size of other skull characters increased with increasing latitude.

It is possible that our methods did not measure the full capacity of Michigan red squirrels to extract energy from hard mast items. Individuals were presented with a single item of each food type, thus precluding the opportunity to improve efficiency via learning (Weigl and Hanson 1980). However, the aforementioned differences in cranial morphology between regions strongly suggest that greater efficiency of use by Indiana red squirrels for black walnuts and bur oak acorns was largely due to larger cranial characteristics.

There may be a time component to differences in efficiency of resource use and cranial morphology associated with the recent invasion of the red squirrel into the central hardwoods region. The longer an ecologically flexible species exists in an environment in which it was historically absent, the more features under selective pressure should be expected to change to match that environment (Benkman 1993). While it is not possible to calculate the efficiency of food utilization for individuals in past years, morphological examina-

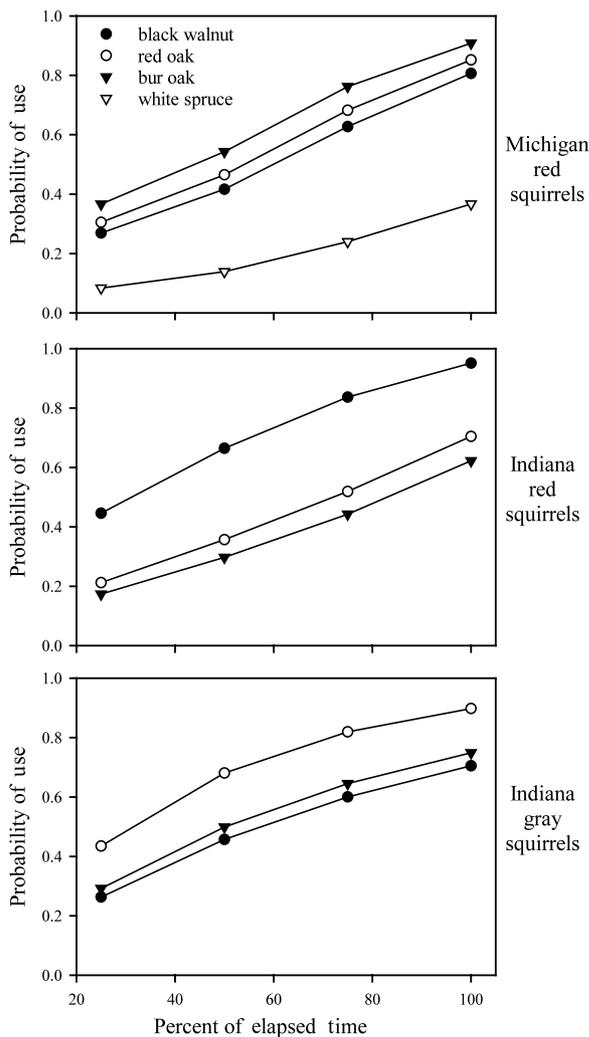


Fig. 5. Best-fitting proportional hazards models for Michigan red squirrels (top), Indiana red squirrels (middle), and gray squirrels (bottom) as a function of food item type. Michigan red squirrel model: $P = 1 - \exp\{-[\exp(-4.379 + 0.150X_1 + 0.375X_2 - 1.280X_3)]t\}$ where variables $X_1 - X_3$ are dummy variables designating food type (000 = black walnut, 100 = red oak, 010 = bur oak, 001 = white spruce); Indiana red squirrel model: $P = 1 - \exp\{-[\exp(-4.877 + 0.2250X_1 + 1.131X_2)]t\}$ where variables $X_1 - X_2$ are dummy variables designating food type (00 = bur oak, 10 = red oak, 01 = black walnut); gray squirrel model: $P = 1 - \exp\{-[\exp(-4.218 + 0.4000X_1 - 0.2750X_2)]t\}$ where variables $X_1 - X_2$ are dummy variables designating food type (00 = black walnut, 10 = red oak, 01 = bur oak). For all three models, t is the percentage of the trial that had elapsed.

tion of specimens collected at different times provides a reasonable surrogate measure. Examination of Figs. 3 and 4 reveals that, while not statistically significant, some time related changes in morphology may exist. The slopes of the lines in Fig. 3 suggest a slight tendency for Indiana squirrel head sizes to increase through time. Fig. 4 suggests body size differences between Indiana and Michigan red squirrels have not

changed through time. However, the increase in head size in light of constant body size supports the hypothesis that the need for greater efficiency in processing hard mast is greater in hardwood-dominated environments. A larger sample, more evenly dispersed through time, will be required to thoroughly evaluate this hypothesis.

Contrary to predictions of the prior exposure hypothesis (Table 1), Michigan red squirrels avoided spruce cones in our field trials of diet preference. Black walnuts and, to a lesser extent, red oak acorns were preferred over other types of food items. These preferences were similar to preferences of Indiana red squirrels, which also selected black walnuts and avoided white spruce cones. This result was somewhat surprising, given the influence of habitat upon diet selection documented in previous studies (Werner and Hall 1979, Briggs and Smith 1989). In addition, our results were not supportive of the hypothesis that resource preferences were driven by the rate of energy extraction (kJ/min; Table 1 and 5). For Michigan red squirrels, the preference for black walnut despite poor efficiency of use suggests that cues driving resource preferences may be innate and unrelated to the energy extracted per unit time.

At northern latitudes, over-winter survival of red squirrels is dependent upon procurement and preservation of food resources, specifically quality of the central midden (Larsen and Boutin 1994). Red squirrels are larderhoarders throughout the majority of their range (Hatt 1943, Smith 1981), although individuals in the eastern part of the range commonly scatterhoard food items (Layne 1954, Dempsey and Keppie 1993, Hurly and Lourie 1997). Survival of individuals and resulting persistence of populations likely is dependent upon the

Table 5. Caloric content and rates of metabolizable energy extraction for food item types used in our study.

	kJ/g dry mass ^a	Mean metabolized kJ/min ^b
Black walnut		
Indiana red squirrel	26.066	2.278 ± 0.726
Michigan red squirrel		0.006 ± 0.011
Gray squirrel		5.298 ± 2.063
Red oak	20.367	
Indiana red squirrel		8.574 ± 3.552 ^c
Michigan red squirrel		6.361 ± 4.564 ^c
Gray squirrel		14.031 ± 2.692
Bur oak	18.158	
Indiana red squirrel		5.877 ± 2.034
Michigan red squirrel		3.726 ± 1.40
Gray squirrel		11.619 ± 3.857
White spruce	27.677	

^a Brink et al. 1966, Smith and Follmer 1972, Lewis 1982.

^b Multiplied kJ extracted/min by the % metabolizable energy per food type. From Smith 1970, Smith and Follmer 1972.

^c Used % metabolizable energy estimates for *Quercus shumardii*, a species in the same subgenus (*Erythrobalanus*) as red oak.

perishability of seeds, such that decisions involving food preference or selection may reflect the strong effect of perishability on fitness (Frank 1988, Vander Wall 1990, Gendron and Reichman 1995, Hadj-Chikh et al. 1996). Neither Michigan nor Indiana red squirrels preferred food items yielding a greater energy return per unit time (Table 4), and Michigan red squirrels did not prefer food items of greater familiarity (i.e. white spruce cones). Our data most strongly support the idea that perishability is the predominant factor driving diet preferences in red squirrels (Table 1).

Red squirrels at our study sites in Indiana occasionally construct larderhoards (Goheen and Swihart, pers. obs.). At northern latitudes, the preservation of conifer cones is dependent upon elevated levels of humidity as a result of decaying organic matter within larders (Smith 1968, 1970). Larders in Indiana consist solely of black walnuts, even when conifers are abundant, and do not occur in conjunction with piles of decaying organic debris (i.e. middens) characteristic of those at northern latitudes (Goheen and Swihart, pers. obs.). Although we do not know whether red squirrels at our study sites in Michigan actively manipulated perishability of white spruce cones, two lines of evidence suggest that they did not. First, we observed few middens on our study sites in Michigan. Middens we did see were comprised solely of red pine cones and were much smaller in size than those maintained by red squirrels in western North America (Smith 1968, Gurnell 1984). Second, we gathered additional observational information of food item preferences in 2001 to supplement our resource-preference trials. Although we could not document precisely the fate of food items that were carried out of view by squirrels, 62% (8 out of 13) of white spruce cones were eaten immediately in the vicinity of the feeding station. In contrast, only 11% (10 out of 88) of bur oak acorns, 14% (13 out of 96) of red oak acorns, and 0% (0 out of 98) of black walnuts were consumed in close proximity to the feeding stations. These proportions are conservative, because, with the exception of those items eaten in the vicinity of feeding stations, we could not document unequivocally the fate of food items in Michigan. When presented with foods of varying perishability, animals should cache items that are less perishable and consume items that are more perishable (Smallwood and Peters 1986, Hadj-Chikh et al. 1996). Red squirrels were more likely to consume white spruce cones than hoard them, suggesting that white spruce cones are not actively managed by red squirrels and thus are of higher perishability at our study sites relative to other food items. Further, it is highly unlikely that food items carried out of view were being consumed, given < 3 minutes elapsed between successive visits to feeding stations and individuals used in handling-time trials spent 52.68 ± 11.93 min, 10.82 ± 5.48 min, and 8.44 ± 2.93 min processing black walnuts, red oak acorns, and bur oak acorns, respectively.

Despite this evidence that perishability seemingly drives diet preferences, we present two alternative possibilities. First, animals may consume those foods with the lowest handling times and cache those foods with the highest handling times (Jacobs 1992, Thomas and Weigl 1998). This should be most pronounced in times of resource abundance (i.e. summer and fall months; Thomas and Weigl 1998). Second, it also is possible that selection of nuts by red squirrels from Michigan is a maladaptation, given the poor efficiency of use of nuts relative to white spruce cones. Resource preferences may be dictated by chemical cues or sensory responses to flavors, such that maladaptive preferences for novel food items may be noted if these food items are associated with chemical cues, flavors, or other stimuli (Galef 1996).

Rates of energy extraction were greater for gray squirrels than red squirrels in Indiana (Fig. 2), which is not surprising given the difference in size between the two species. More importantly, gray squirrels appear to be more efficient than red squirrels at using nuts, even after correcting for species-specific differences in metabolic requirements. Average daily assimilation and metabolic rates for adult gray squirrels in autumn are 530 kJ and 416 kJ, respectively (Koprowski 1994). Daily assimilation rates for adult red squirrels are 340 kJ (Steele 1998). Assuming that the relation between assimilated and metabolizable energy is the same for both species, red squirrels need to extract energy 0.64 times as fast as gray squirrels to attain their daily energetic needs as efficiently (i.e. in the same amount of foraging time). Based on the data in Fig. 2 and Table 4, we corrected for species-specific differences in daily energy requirements. Indiana red squirrels were 35%, 10%, and 17% less efficient than gray squirrels at using black walnut, red oak, and bur oak, respectively. This suggests that, although variation in the efficiency of energy extraction differed between deciduous and coniferous environments, red squirrels in Indiana still were inferior to gray squirrels in this regard. The lower efficiency of resource use by red squirrels, coupled with larderhoarding of black walnuts, implies that red squirrels will be unable to compensate completely for the functional role filled previously by gray squirrels in fragmented areas of the central hardwoods.

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