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Food-hoarding behavior of gray squirrels and North American red squirrels in the central hardwoods region: implications for forest regeneration

Jacob R. Goheen and Robert K. Swihart

Abstract: The North American red squirrel (*Tamiasciurus hudsonicus*) has expanded its geographic range into the state of Indiana concurrently with a decline in populations of gray squirrels (*Sciurus carolinensis*) throughout portions of the central hardwoods region of the United States that have been converted to intensive agriculture. Red squirrels construct larder hoards and function as seed predators throughout much of their geographic range. In contrast, gray squirrels construct scatter hoards and thus function as seed dispersers in addition to eating seeds. We conducted field observations to discern whether hoarding behavior differed between the two species in a deciduous forest stand near the southern limit of the range of red squirrels. Red squirrels were more likely to hoard walnuts and acorns in larders or trees, whereas gray squirrels were more likely to scatter-hoard mast items. We present a simple model to illustrate the potential impact of interspecific differences in hoarding on germination success of black walnut. Our results suggest that red squirrels are unable to compensate completely for the loss of gray squirrels as seed dispersers in portions of the central hardwoods region that have been transformed by agriculture.

Résumé : L'écureuil roux d'Amérique du Nord (*Tamiasciurus hudsonicus*) a étendu sa répartition géographique jusque dans l'état d'Indiana, concurremment au déclin de l'écureuil gris (*Sciurus carolinensis*) dans les régions de la forêt centrale des bois durs des États-Unis qui ont été transformées en zones d'agriculture intensive. Les écureuils roux se construisent des caches alimentaires comme garde-manger et ils sont donc des prédateurs de graines sur la plus grande partie de leur aire de répartition. Les écureuils gris, au contraire, construisent des caches éparpillées et ils servent donc à disperser les graines, bien qu'ils en consomment une partie. Des études de terrain nous ont permis de vérifier si le comportement d'approvisionnement diffère chez les deux espèces dans un boisé de forêt décidue près de la limite australe de la répartition géographique des écureuils roux. Les écureuils roux sont plus susceptibles d'accumuler des noix et des glands dans leurs caches ou dans les arbres, alors que les écureuils gris sont plus susceptibles de disperser des éléments de la faînée. Nous présentons un modèle simple qui illustre l'impact potentiel des différences interspécifiques d'approvisionnement sur le succès de la germination du noyer noir. Nos résultats montrent que les écureuils roux sont incapables de remplir adéquatement le rôle joué antérieurement par les écureuils gris dans la dispersion des graines dans les régions de la forêt centrale de bois durs qui ont été modifiées par l'agriculture.

[Traduit par la Rédaction]

Introduction

The North American red squirrel (*Tamiasciurus hudsonicus*; hereinafter red squirrel) has expanded its geographic range into the state of Indiana in conjunction with increasing fragmentation of forests due to agriculture and decreasing populations of gray squirrels (*Sciurus carolinensis*), a native competitor that is sensitive to forest fragmentation (Nixon 1978; Mumford and Whittaker 1982; Nupp and Swihart 2000, 2001; Goheen et al. 2003*a*). Throughout much of its range, the red squirrel hoards food items in a central location (i.e., larder hoarding; Steele 1998), although individuals in the eastern part of the range commonly scatter-hoard foods (Layne 1954; Dempsey and Keppie 1993). Larder hoarding

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is thought to have coevolved with territoriality in the species, and larders are defended throughout the year (Smith 1968; Steele 1998). In contrast, the gray squirrel is a scatter-hoarder and does not defend its caches from conspecifics or other potential seed predators (Koprowski 1994).

The coevolutionary ties between scatter-hoarding squirrels and mast-producing trees have been well documented, and gray squirrels are at least partially responsible for the regeneration success of many species of deciduous trees (Steele et al. 1993; Vander Wall 1990, 2001). Establishment of animal-dispersed seeds may be inhibited if primary seed dispersers differ sufficiently in their foraging or hoarding behaviors from other seed dispersers or predators (Hutchins et al. 1996; Li and Zhang 2003). Thus, to the extent that mast-producing trees are dependent upon scatter hoarders for successful recruitment of seedlings, increasing populations of other seed dispersers or predators may negatively affect future forest-regeneration processes.

Given the recent range expansion of red squirrels concurrent with a decline in populations of gray squirrels in Indiana, we were interested in documenting the food-hoarding behavior of both species. We undertook a series of field observations to determine whether or not food-hoarding behaviors differed between red and gray squirrels in Indiana, and if they did, the extent to which this occurred. If red squirrels in Indiana are larder hoarders, they may not be functionally analogous to gray squirrels with respect to facilitating seed dispersal.

Materials and methods

We observed hoarding behavior of red and gray squirrels in a 2.5-ha forest remnant 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 central United States (Mumford and Whittaker 1982). Dominant tree species at the site included oaks (*Quercus* spp.), hickories (*Carya* spp.), maples (*Acer* spp.), and black walnut (*Juglans nigra*). Conifers were present but uncommon at the site.

Field trials of hoarding behavior were conducted from 6 June to 29 June 2000 and from 31 May to 27 June 2001 in conjunction with a larger study to assess differences in resource preferences between red squirrels from deciduous environments in Indiana and those from predominantly coniferous environments in the Upper Peninsula of Michigan (Goheen et al. 2003*b*). For the present study, we were interested in assessing differences in hoarding behavior between red and gray squirrels with respect to three species of mast common to the central hardwoods region and known to be important components of red and gray squirrel diets (Korschgen 1981; Steele 1998): northern red oak (*Quercus rubra*), bur oak (*Quercus macrocarpa*), and black walnut. Secondarily, for those items manipulated by red squirrels, we were interested in whether the fates of black walnuts differed from those of acorns. In our study systems, red squirrels prefer black walnut to other species of hard mast (Ivan and Swihart 2000; Goheen et al. 2003*b*), and the vast majority of red squirrel larder hoards consist solely of black walnuts (J.R. Goheen and R.K. Swihart, personal observations).

Feeding stations were constructed by gluing 4 square petri dishes on a 50 cm × 10 cm piece of plywood, with 3 or 4 items of each mast type in different petri dishes. Petri dishes were spaced about 3 cm apart. Stations were placed in 12 locations separated by ≥200 m, making it highly unlikely that multiple stations were visited by an individual (Layne 1954; J.R. Goheen and R.K. Swihart, unpublished data). Stations were prebaited with sunflower seeds or English walnuts for 1–2 days prior to foraging observations.

Data on fates of mast items were recorded by observers hidden approximately 30 m from feeding stations between 0600 and 1100. On most days, we conducted two bouts of foraging observations simultaneously. Stations used in simultaneous observations were those in closest proximity to one another to further ensure that individuals were not visiting multiple stations. We classified the fate of each mast item as one of the following: (*i*) larder-hoarded if it was cached above ground in a central location with other food items; (*ii*) scatter-hoarded if it was buried below ground and individually; (*iii*) hoarded if it was cached above ground but not associated with a larder (e.g., in the crotch of a tree branch or at the base of a tree); or (*iv*) consumed. A station was monitored until a trial had been recorded for one red squirrel and one gray squirrel, the criterion being that each individual was offered the full complement of mast types from which to choose.

Data on hoarding behavior were analyzed using hierarchical log-linear models with a backward-selection procedure ($\alpha = 0.05$) to examine associations between squirrel species, mast type, and fate of mast items. Because we were most interested in the fate of mast items and consequent implications for tree regeneration, we pooled data into two categories for purposes of analysis: scatter-hoarded and otherwise hoarded (i.e., larder-hoarded or hoarded).

Results and discussion

We recorded the caching behavior of 12 red squirrels and 13 gray squirrels. Of these, one individual of each species only consumed and did not hoard the mast items offered; these individuals were excluded from the analysis. Fates were recorded for 33 walnuts, 24 red oak acorns, and 21 bur oak acorns handled by red squirrels and for 25 walnuts, 36 red oak acorns, and 29 bur oak acorns handled by gray squirrels.

Log-linear analysis revealed a significant effect of mast type ($\chi^2 = 9.13$, df = 1, $P = 0.0104$) and the interaction of squirrel species and fate of mast items ($\chi^2 = 117.17$, df = 1, $P < 0.0001$). This model provided a good fit to the data ($\chi^2 = 7.08$, df = 6, $P = 0.313$). Bur oak acorns (21.5% of the total) were less likely to be hoarded than either red oak acorns (36.9% of the total) or black walnuts (41.5% of the total). Of more interest in terms of impacts on regeneration, red and gray squirrels differed from each other with respect to hoarding of mast items. Most mast items (88.9%) hoarded by red squirrels were larder-hoarded or cached in trees, whereas all but two mast items (96.9%) hoarded by gray squirrels were scatter-hoarded (Fig. 1). Red squirrels were more likely to hoard black walnuts than acorns, and were more likely to eat acorns than black walnuts ($\chi^2 = 8.278$, df = 2, $P = 0.016$). For gray squirrels, no differences existed

Fig. 1. Hoarding and consumption of mast (acorns and black walnuts) by red squirrels (*Tamiasciurus hudsonicus*) and gray squirrels (*Sciurus carolinensis*) in a forest remnant in Indiana within the central hardwoods region. See the text for sample sizes.

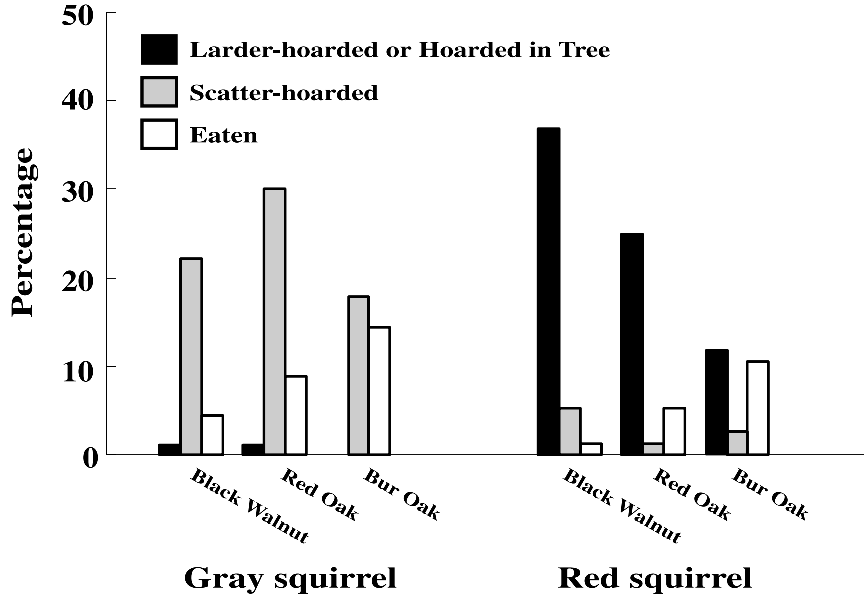
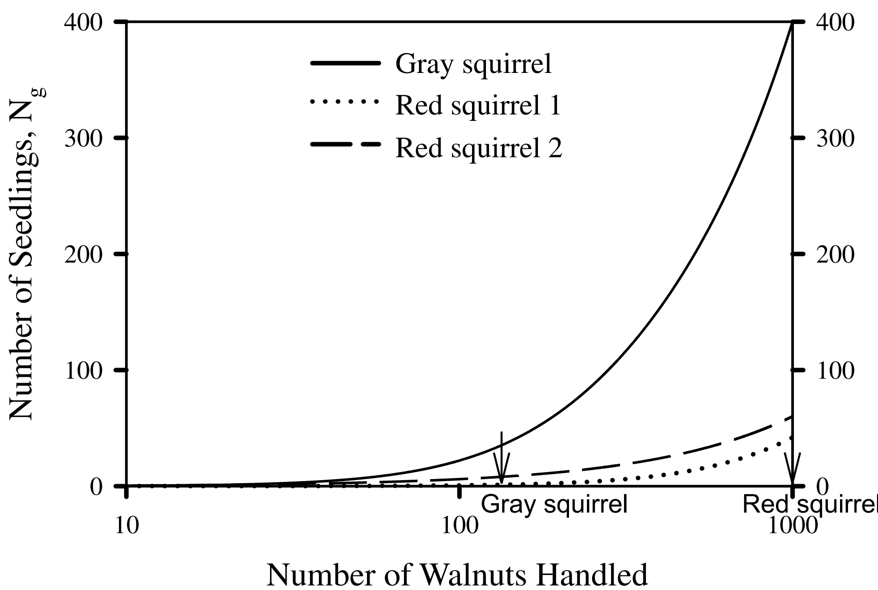


Fig. 2. Predicted numbers of germinating black walnut seedlings (N_g) as a function of the number of walnuts handled by squirrels of the two species. The model describing the relationship is $N_g = N_h p_{sh} p_g\ (1 - e^{-aN_h p_{sh}})$, where p_{sh} is the probability of scatter hoarding a nut, p_g is the probability that a scatter-hoarded nut surviving to the spring will germinate, N_h is the total number of walnuts handled by squirrels during the fall, and a is a decay constant related to changes in the rate of recovery of walnuts as a function of the number scatter-hoarded (i.e., a larger a value indicates poorer recovery). For the results depicted, p_g = 0.5 and p_{sh} = 0.80 for gray squirrels and 0.12 for red squirrels. For red squirrel 1, a = 0.01, whereas for red squirrel 2, a = 1.0. The arrows depict the predicted number of nuts that need to be handled by red and gray squirrels if N_g = 42, when a = 0.01.



between the fates of black walnuts and acorns (χ^2 = 2.715, df = 2, P = 0.257).

What are the implications of our findings for regeneration of forest trees in landscapes where red squirrels appear to be replacing gray squirrels? Burial of nuts by scatter-hoarding animals is highly beneficial, if not necessary, for regeneration of mast-producing trees (Vander Wall 2001). Scatter hoarding simultaneously reduces the probability of seed predation, maintains the viability of seeds, and facilitates germination and establishment of seedlings (Vander Wall 1990). Thus, a shift in the level of scatter hoarding could alter the regeneration success of affected tree species. A simple model serves to illustrate the potential magnitude of the impact of shifts in hoarding behavior on one tree species, black walnut. In general, the number of sound walnuts that survive to germinate the following spring, N_g, can be expressed as $N_g = N_h p_{sh}(1 - p_{r|sh})p_g$, where N_h is the number of walnuts handled by squirrels during fall, p_{sh} is the per-nut probability of being scatter-hoarded, given that it was handled by a squirrel, $p_{r|sh}$ is the per-nut probability of being recovered by a squirrel, given that it was scatter-hoarded, and p_g is the probability of germination for a scatter-hoarded walnut surviving to spring. Our study provides preliminary estimates of p_{sh} for gray squirrels (0.80) and red squirrels (0.12). A p_g value of 0.50 was used, based on data in Young and Young (1992, p. 185). We assumed that the probability of recovery of an individual nut was inversely related to the number of scatter-hoarded nuts according to the functional form $p_{r|sh} = \exp(-aN_{sh})$, where a is a constant quantifying the rate at which recovery decays with N_{sh}, the number of walnuts scatter-hoarded. Using other functional forms for density-dependent recovery would alter our conclusions quantitatively but not qualitatively.

The number of germinating walnuts predicted from this simple model is plotted against N_h in Fig. 2. Several outcomes are noteworthy. First, assigning comparable recovery rates ($p_{r|sh}$) for the two species of squirrels results in a predicted level of germination success that increases with N_h and, over the range of N_h we used, is greater by at least an order of magnitude when nuts were handled by gray squirrels. Put another way, interspecific differences in the propensity to scatter-hoard walnuts would require red squirrels to handle 1000 walnuts to achieve the same germination success that results from the handling of 150 walnuts by gray squirrels (arrows in Fig. 2). Of course it is possible that red squirrels might recover fewer buried nuts than gray squirrels, either because they have a less well developed spatial memory than gray squirrels or because red squirrels may experience greater difficulty physically recovering buried nuts when the ground is hard or frozen. To account for this possibility, we reduced the rate of recovery by red squirrels by increasing the density-dependent decay term, a, by two orders of magnitude. Reducing recovery success to this degree yielded only modest improvements in walnut germination success (Fig. 2), emphasizing the importance of the interspecific differences in hoarding tendencies.

Our results suggest that if red squirrels are able to colonize and persist in the fragmented landscapes of northern Indiana in response to decreasing numbers of gray squirrels, they may not compensate completely for the loss of the gray squirrels that previously filled this functional role (sensu Huston 1994). Further research is necessary to determine the generality of our findings, and how interspecific differences in hoarding and recovery behavior interact with forest fragmentation and tree-species composition and competition (Nupp and Swihart 2001) to affect the structure of forest communities in the central hardwoods region.

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