

## Foraging Patterns of Eastern Gray Squirrels (*Sciurus carolinensis*) on Goldenrod Gall Insects, a Potentially Important Winter Food Resource

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**ABSTRACT.**—We document the use of goldenrod (*Solidago* spp.) gall insects by eastern gray squirrels (*Sciurus carolinensis*) as a winter food resource. We also examined the foraging patterns of gray squirrels on these gall insects by presenting goldenrod gall feeders at ten sites around Hamilton, New York, during the winters of 1996–1997 and 1997–1998. We predicted that squirrels would attack larger-than-average galls among those presented because larger galls are more likely to contain the larger fly larvae (*Eurosta solidaginis*), rather than the smaller parasitoid (*Eurytoma gigantea*) or nothing at all. Squirrels attacked galls at least once at 6 of the 10 sites where gall feeders were maintained. Galls at feeders were attacked from 11 February to 17 April, and the number of separate attacks on galls at a particular site ranged from 1 to 17. We detected no evidence that squirrels preferentially attacked galls of a particular size class (small, medium, large). There was no indication that squirrels attacked increasingly larger-than-average galls over the duration of the study, which would be expected if squirrels were learning by positive reinforcement. Our results suggest either (1) that squirrels are unable to discriminate among food rewards in galls of different sizes or (2) that all gall insects, regardless of size, provide an important dietary supplement for squirrels during the winter.

### INTRODUCTION

The diet of the eastern gray squirrel (*Sciurus carolinensis*) consists primarily of tree seeds, flowers and fruits from a variety of plants (Nixon *et al.*, 1968; Korschgen, 1981). During the winter, however, squirrels must rely heavily on food caches (primarily acorns and nuts) buried during the autumn. Food limitation may occur in some winters if the autumn nut crop is poor or exhausted early (Koprowski, 1991). Thus, the availability of alternative foods during the winter is likely critical to the survival of squirrels and may be a determinant of female fecundity in the spring.

Although insects may represent an important component of the diet of gray squirrels during the spring and summer (Nixon, 1970; Korschgen, 1981), little is known about the importance of insects at other times of the year. Gray squirrels are known to consume weevils (Coleoptera: Curculionidae) that infest acorns (Weckerly *et al.*, 1989). Although not likely a primary energy source, weevils probably provide squirrels with an important dietary supplement of nitrogen and phosphorus during the autumn and winter. Here we report on the use of goldenrod (*Solidago* spp.) gall insects as a winter food source by eastern gray squirrels. We show that squirrels actively seek gall insects, rather than preying on them incidentally, and argue that gall insects may be an important winter food resource to squirrels.

Larvae of the goldenrod gall fly (*Eurosta solidaginis*) are attacked by a variety of parasites and predators. During the summer, two species of chalcid wasp (*Eurytoma obtusiventris* and *E. gigantea*) parasitize the fly larvae early in the life cycle (Uhler, 1951). Birds such as downy

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woodpeckers (*Picoides pubescens*) and black-capped chickadees (*Parus atricapillus*) open galls and extract the inhabitants during the winter when other food is scarce (Cane and Kurczewski, 1976; Schlichter, 1978). Larvae of the beetle, *Mordellistena unicolor* also may prey upon *E. solidaginis* larvae before winter diapause (Weis and Abrahamson, 1985, *pers. obs.*). The eastern gray squirrel is a previously undocumented predator in this system.

The parasitic wasp *Eurytoma gigantea* attacks galls after reaching maximum size in late summer (Weis and Abrahamson, 1985) but is limited to attacking smaller galls because of its small ovipositor (Weis *et al.*, 1985). Conversely, predatory birds preferentially attack larger galls (Moeller and Thogerson, 1978; Walton, 1988), most likely because they have a higher probability of finding the larger gallfly larvae (ca. 0.05 g) rather than the smaller wasp larvae (ca. 0.01 g), or because birds can gain access through the exit tunnel prepared by the gallfly larvae (Confer and Paicos, 1985; Confer *et al.*, 1986). Fly larvae are parasitized before they excavate the tunnel; thus, birds must chisel their own hole into a parasitized gall which takes more time and energy and results in a smaller reward.

During the winter and early spring of 1997 and 1998 we established several feeding stations containing upright goldenrod (*Solidago altissima*) stems with galls to explore questions regarding the foraging strategies of birds. However, squirrel predation at six of the sites provided a unusual opportunity to study the foraging patterns of this predator on a novel food source. We predicted that squirrels would attack larger-than-average galls, as do birds.

#### METHODS

*Preliminary analyses.*—During the winter of 1996–1997 we harvested goldenrod galls randomly from each of five gridded fields in central New York. Samples (>200 galls at each site) were collected by establishing 40 m linear transects, with starting point and direction determined by a random-numbers table and compass, respectively. All galled stems encountered within 0.5 m of the transect line were collected and brought to the laboratory. Gall diameters were measured using an incremental (0.2 mm) series of circle templates. Galls were then dissected and the occupant (if any) was determined (*see* Uhler, 1951; Zurovchak and Shealer, 1996, for identification criteria). All living gall occupants were weighed to the nearest 0.1 mg.

Gall diameters were compared statistically using a two-way analysis of variance (ANOVA), with field ( $n = 5$ ) and fate (surviving gallfly larva, parasitized by *Eurytoma gigantea*, or preyed upon by birds) as main effects. This analysis confirmed that *E. gigantea* preferentially parasitizes smaller galls and birds attack larger galls (overall  $F_{13,756} = 23.5$ ,  $P < 0.001$ ; gall size according to fate compared by Tukey-Kramer tests, surviving gallfly larvae = bird predation > parasitized), as found in earlier studies (Cane and Kurczewski, 1976; Weis *et al.*, 1985). No differences in parasitism and predation levels were found among fields, and the interaction term (field  $\times$  fate) was likewise not significant (both  $P > 0.05$ ).

Mean ( $\pm$ SE) mass of third-instar *Eurosta solidaginis* larvae was  $44.2 \pm 0.4$  mg ( $n = 599$ ); mean mass of *Eurytoma gigantea* larvae was  $9.4 \pm 0.5$  mg ( $n = 154$ ). This difference was highly significant ( $t_{743} = 39.3$ ,  $P < 0.0001$ ). When all living gall occupants were considered in the field samples, a significant difference was found between occupant mass and the sizes of galls they occupied ( $F_{2,1401} = 56.1$ ,  $P < 0.001$ ). Tukey-Kramer tests revealed that the mass of gall insects occupying large ( $34.4$  mg  $\pm$  1.3 SE;  $n = 236$ ) and medium ( $33.5 \pm 0.9$ ;  $n = 490$ ) sized galls did not differ, whereas both were significantly ( $P < 0.05$ ) greater than occupants in small ( $22.7 \pm 0.8$ ;  $n = 678$ ) galls. Moreover, small galls were more likely to be empty (32.8%,  $n = 668$ ) than either medium (14.6%,  $n = 501$ ) or large (10.5%,  $n = 257$ ) galls ( $X^2 = 80.1$ ,  $df = 2$ ,  $P < 0.001$ ). The above analyses of gall size and occupant

TABLE 1.—Sites where goldenrod gall feeders were attacked, year and date of presentation, and summary information on attacks by squirrels

Site	Year	Date of first presentation	Time to first attack (d)	First and last attack dates	No. of times feeder attacked	Attack interval (d) ( $\bar{x} \pm \text{SD}$ )
Payne Street	1997	15 Feb.	16	2 Mar.–7 Apr.	17	1.0 $\pm$ 0.5
Hill Road	1997	15 Feb.	8	23 Feb.–16 Apr.	7	7.0 $\pm$ 3.6
Dietz <sup>1</sup>	1997	10 Feb.	1	11 Feb.–11 Feb.	1	—
Novak	1997	19 Jan.	24	11 Feb.–11 Feb.	1	—
Novak	1998	29 Jan.	58	28 Mar.–17 Apr.	2	—
Olin east	1998	20 Feb.	3	23 Feb.–28 Mar.	2	2.0 $\pm$ 1.5
Olin south	1998	20 Feb.	16	8 Mar.–8 Mar.	1	—

<sup>1</sup> Abandoned as a study site following the first attack

mass indicate that bird and mammal predators generally should expect a larger reward in a larger gall, and that larger galls were less likely to be empty.

*Feeder experiment.*—Single feeders containing goldenrod galls were maintained at 8 sites from 19 January to 16 April 1997, and at four sites (including two sites used in 1997) from 29 January to 17 April 1998. All feeder sites were located in and around the town of Hamilton, Madison Co., New York (Table 1). Most gall feeders ( $n = 8$ ) were established at sites with bird feeders and were far enough apart ( $>0.5$  km) to ensure that different animals were visiting them. Although not territorial (Thompson, 1978; Don, 1983), gray squirrels typically occupy home ranges  $<5$  ha (Flyger and Gates 1982; Don, 1983). Each feeder contained 36 goldenrod stems each supporting a single gall. Stems were inserted into holes drilled into a wooden base ( $60 \text{ cm}^2$ ) and spaced equidistantly (10 cm apart) in rows and columns. Because ground-to-gall height has been shown to affect foraging preferences of woodpeckers (Cane and Kurczewski, 1976), stems were cut so that all galls were between 25 and 30 cm from the ground.

Since gall formation does not occur on goldenrod without an insect stimulus, we assumed that all galls used in the feeders contained an insect, whether living or dead. *Eurosta solidaginis* larvae occasionally die early, but there is no way to discern by external examination the gall occupant or its fate. The larval gall fly chews an exit tunnel from the central chamber to the gall epidermis before winter diapause (Uhler, 1951), but this tunnel remains covered by a thin layer of plant tissue and is not apparent by external examination. Adult gall flies emerge in mid to late May, with the parasitoids emerging later (Uhler, 1951). Therefore, during the periods of our study, all gall insects were still larvae or pupae.

The exact diameter (to the nearest 0.2 mm) of each gall presented was measured. Galls were grouped into three relative size classes according to their maximum diameter: small ( $<2.1$  cm), medium (2.1–2.4 cm) and large ( $>2.4$  cm). Equal numbers (12) of stems bearing galls of each size class were randomly inserted into known position in each feeder.

Feeders were set out in the evening or early morning and examined in the late afternoon of the same day. Feeders that were attacked by predators were replaced within an hour of discovery, such that galls were available almost continually at each site. Following each attack, the area surrounding the feeder was searched for the attacked galls. Galls were classified as attacked by squirrels if they were severed from the stem, or if they showed signs of teeth marks (Fig. 1). Successful attacks were defined as galls that showed signs of being chewed and the occupant was missing. In many situations, galls were severed from stems with only fragments of plant tissue on the ground; these also were scored as successful

attacks. Although birds attacked galls at several feeders, all data contained herein include only those feeders that were attacked exclusively by squirrels. We chose to use all rather than just successful attacks as our response variable, because in many cases galls were completely destroyed by predators and we could not be certain that the occupant was consumed. We believed that attacks are sufficient to demonstrate intent by the predator, whether or not the attack was successful.

For feeders attacked only once ( $n = 5$ ), we treated each feeder as an independent replicate and used a Kruskal-Wallis test to compare the percent use ( $n$  attacked/ $n$  available) of galls from each size class. The nonparametric test was chosen because the response variable was resistant to normalizing transformation. For feeders attacked more than twice ( $n = 2$ ), we used a repeated-measures ANOVA to determine differences in percent use as a function of site, replicate or gall size. To meet normality assumptions, the response variable (percent use) was arcsine-transformed before analysis (Zar, 1974). For the two feeders that were attacked repeatedly, we used regression statistics to determine if gall size preferences by squirrels changed in a predictable manner over time. For this analysis, we subtracted the mean diameter of all galls presented at a particular feeder from the diameter of each gall that was attacked. Thus, attacked galls were assigned positive (larger than mean), zero (equal to mean) or negative (smaller than mean) values, allowing us to control for differences in mean gall size among feeders. Statistical significance for all tests was accepted at a  $P < 0.05$ .

## RESULTS

Squirrels attacked gall feeders at least once at six of the ten different sites where feeders were presented. All six of these feeder-sites were at established bird feeding stations where squirrels were present and feeding before our experiments, as were two of the four gall feeders that were never attacked. The other two gall feeders that were not attacked bordered woodlots where no bird feeders were established, but where squirrels were present. Examination of galls following attacks by squirrels indicated that they consumed both the gallfly larvae and wasp parasitoids (*Eurytoma gigantea* and *E. obtusiventris*).

For all feeders combined ( $n = 31$  total), the mean ( $\pm$ SD) number of galls attacked per feeder was  $14.5 \pm 9.3$  (range 1–36). Both the frequency of attacks on gall feeders and the intervals between attacks differed among sites (Table 1). At most sites, gall feeders were available to squirrels for at least two weeks before attacks began; however, at one site (Dietz), squirrels attacked all 36 galls within a day of the feeder's first presentation. The pattern of attacks at the two most frequently-attacked feeders differed: at one site (Payne St.) the feeder was attacked almost daily, whereas another (Hill Road) was attacked less frequently (Table 1). We counted as many as six squirrels present near the feeders, but we do not know how many were involved in attacking goldenrod galls.

Videotaped attacks ( $n = 3$ ) by squirrels at one feeder suggested that most attacks occurred as follows. The squirrel reared up on its hind legs, grasped a goldenrod stem in both forepaws and pulled the gall toward its mouth. It chewed the stem just below the gall, leaving only the gall in its front paws. Then the squirrel chewed through the gall tissue until it reached the central chamber, whereupon it ate the occupant. Evidence at other sites (stems without galls, fragments of plant tissue on the ground) suggests that this behavior was used to attack the majority of galls. With the exception of birds, no other predator was observed or suspected to prey upon gall insects. All footprints in the snow and the sizes of incisor marks on the galls indicated that squirrels were the only mammalian predator at the gall feeders (Fig. 1).

For the five feeders that were attacked only once (Table 2), squirrels attacked galls of

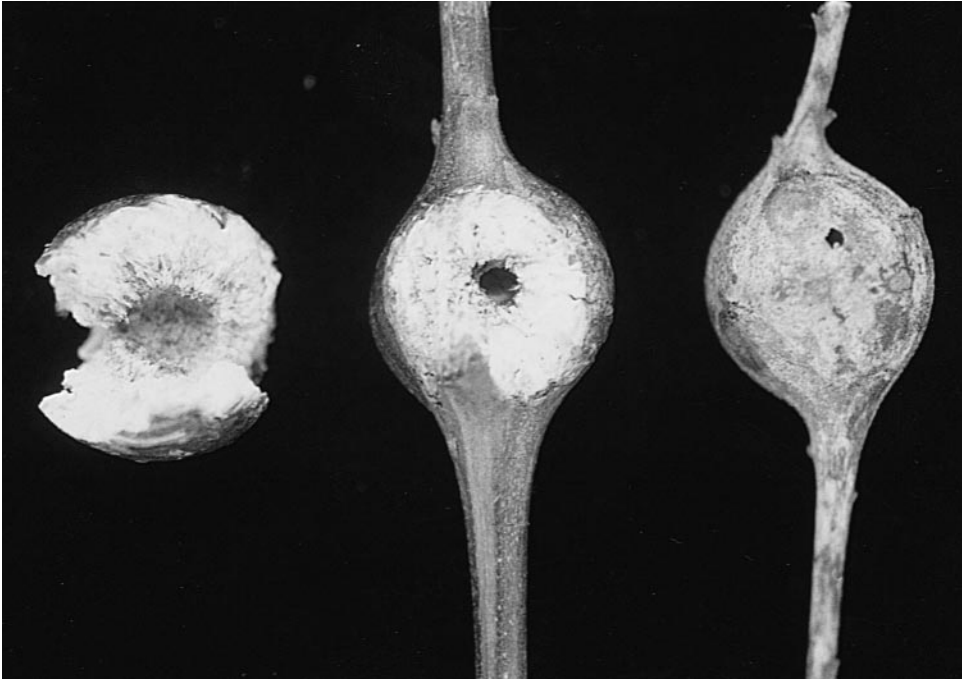


FIG. 1.—Typical gall characteristics following attack, from left to right, by gray squirrels, black-capped chickadees and downy woodpeckers. Note the jagged teeth marks left by squirrels, the removal of much of the epidermal tissue by chickadees and the small and precise hole made by woodpeckers. Only squirrels severed galls from the stem

each size class equally in proportion to their availability (Kruskal-Wallis  $X^2 = 0.02$ ,  $df = 2$ ,  $P > 0.95$ ). At the two sites where feeders were attacked more than twice (Payne Street, Hill Road), replicate was the only significant effect (repeated measures ANOVA,  $F = 2.35$ ,  $P < 0.01$ ). Site ( $F = 0.0$ ,  $P > 0.95$ ), gall size ( $F = 0.40$ ,  $P > 0.50$ ), or any of the interaction terms were not significant. Although replicate was a significant effect in the model, regression analyses comparing the difference of each attacked gall from the mean versus date of attack for Payne Street ( $R^2 = 0.041$ ) and Hill Road ( $R^2 = 0.044$ ) indicated that the slope of the line did not differ significantly ( $P > 0.50$  for each site) from zero at either site. Thus,

TABLE 2.—Mean ( $\pm$  SE) percent use (n galls attacked/n galls presented) for each gall size class (small, medium, large) at the Payne Street site (n = 17 separate attacks), Hill Road site (n = 5 attacks), and all other feeders (n = 5) that were attacked only once each

Site	Gall size		
	Small	Medium	Large
Payne Street	51.0 $\pm$ 7.7	53.4 $\pm$ 9.2	62.3 $\pm$ 7.6
Hill Road	31.7 $\pm$ 3.1	28.3 $\pm$ 12.5	36.7 $\pm$ 13.1
All other	43.3 $\pm$ 15.5	43.3 $\pm$ 13.3	46.7 $\pm$ 10.7

there was no evidence that squirrels attacked increasingly larger galls over the period of our study.

#### DISCUSSION

Our results indicate that gray squirrels around Hamilton, New York, use goldenrod gall insects as a food resource during the winter and early spring. The broad geographic range of *Eurosta solidaginis* and its associated parasitoids (New Brunswick to Texas to British Columbia; Wasbauer, 1972) suggests that these insects are potentially available as winter food to squirrels in many areas of North America. To our knowledge, however, our study is the first to document the use of goldenrod gall insects by squirrels. The somewhat artificial nature of gall presentation (most were near backyard bird feeders) may have facilitated predation by squirrels; at most feeders a week or more elapsed before the first attack, suggesting that squirrels may not have inherently recognized galls as containing food but learned quickly by trial-and-error sampling.

The diet of gray squirrels consists mainly of tree seeds, fruits and nuts (Smith and Follmer, 1972; Mollar, 1983). Insects are eaten in small quantities throughout the year (Nixon *et al.*, 1968), but may be particularly important for juveniles in spring and summer (Nixon, 1970; Korschgen, 1981). Squirrels are known to eat weevils that infest acorns (Weckerly *et al.*, 1989; Steele *et al.*, 1996) and to open acorn galls formed by a cynipid wasp, both in North America (Nixon, 1970) and among captive squirrels in England (Gurnell, 1987). However, little is known about the availability or importance of insects to squirrels in the fall and winter.

Goldenrod gall insects represent an accessible and potentially important food resource to squirrels in the winter when acorn stores are depleted and other food is scarce. Late winter is a critical time for squirrels, particularly for females that are pregnant or lactating. Gall insects may provide squirrels with a relatively high energy reward at little cost, or provide limiting nutrients such as nitrogen and phosphorus that are lacking in acorns. Although goldenrod galls contain high concentrations of phenolics (Abrahamson *et al.*, 1991), our observations indicated that squirrels do not actually eat the gall tissue. Rather, squirrels have learned to chew apart the gall tissue to obtain the fly larvae, primarily composed of phospholipids and triacylglycerols, particularly in the late fall when they are synthesizing cryoprotectants (Bennett *et al.*, 1997).

We found no evidence that squirrels at our feeding stations attacked large galls more than the other two size classes. Moreover, at the two sites where feeders were attacked consistently, squirrels apparently did not develop any preferences for larger galls over the period of time that we conducted these feeding trials. Predatory birds preferentially attack larger galls, probably because large galls are less likely to be parasitized by the much smaller wasp, *Eurytoma gigantea* (Confer and Paicos, 1985; Confer *et al.*, 1986), or empty (this study). Before winter diapause, unparasitized gall fly larvae excavate exit tunnels that birds use to gain easy access to the larvae (Uhler, 1951). Therefore, larger galls provide greater food rewards that are easier to obtain.

We expected that squirrels would quickly adopt a similar strategy of attacking larger galls after sampling the rewards from galls of different sizes, but we found no evidence of this in our study. Our experiments were conducted at outdoor feeding stations where bird seed was supplied continuously. Therefore, food availability at these locations was high throughout the winter. Experiments have shown that animals are more selective when prey availability is high or predictable and less selective when prey are scarce (Krebs *et al.*, 1977; Davidson, 1978; Ringler, 1979; Anderson, 1984). We therefore created the potential for squirrels in our study to exhibit preferences for galls that provided the greatest rewards,

but they failed to do so. The continued sampling of smaller galls by squirrels may relate to the ease by which squirrels can open galls—several seconds compared to several minutes for woodpeckers (Confer *et al.*, 1986).

Our study failed to find evidence that squirrels consistently attacked galls that provided the greatest reward. We conclude that either (1) squirrels are unable to discriminate among galls of different sizes and hence the size of the food reward contained within; (2) the difference in reward (fly larva versus parasitoid) is negligible relative to the ease by which squirrels can open galls; or (3) all gall insects, regardless of size, provide for squirrels during the winter an important dietary supplement of nitrogen and phosphorus, both of which occur in low concentrations in acorns. Our results should be viewed cautiously because the possibility that the same squirrels were not involved in all attacks at each site. Attacks by naive squirrels that located the feeders in the middle of our experiments could have hidden true preferences of more experienced squirrels. A more definitive experiment that better addresses the question of learning ability would be to use individually marked or captive squirrels in a more controlled environment.

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