DOWNY WOODPECKER REWARD RATES FROM GOLDENROD GALL INSECTS

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Field studies of Downy Woodpeckers (*Picoides pubescens*) foraging on the insects in goldenrod galls have reached several conclusions. The Downy Woodpecker prefers to use the exit tunnel prepared by the larvae of the fly *Eurosta solidaginis* to extract the larva (Moeller and Thogerson 1978, Confer and Paicos 1985). They prefer to chisel into galls which contain the larger fly larva rather than galls which contain smaller predacious insects or no insect at all (Schlichter 1974; Moeller and Thogerson 1978, Confer and Paicos 1985). Galls in which the fly larva has been preyed upon by other insects lack an exit tunnel (Uhler 1951). Confer and Paicos (1985) proposed that the Downy Woodpecker is more likely to abandon a gall if unable to locate the exit tunnel.

In these previous field studies, the authors speculated that the Downy Woodpecker's behavior might enhance the rate of obtaining food as follows. Extraction of the fly larva through the exit tunnel requires only locating the tunnel and a peck through the plant epidermal cells covering the tunnel, which may be faster than chiseling a conical hole through the entire gall wall. Abandoning galls when an exit tunnel is not found and, thus, when the gall is more likely to contain a predacious insect may enhance the reward rate, since the predacious insects weigh about ⅛ as much as a fly larva. In this study the reward rates for these behaviors were observed with a caged Downy to test if these speculations were correct.

Methods

An after-hatch-year male Downy Woodpecker was caught in November 1983 and retained in a 1.2x1.2x2.4 m flight cage. Data were obtained on 15 dates from 11 January to 20 March 1984. On non-experimental days the bird received about 10 meal worms (*Tenebrio*) daily with an *ad libidum* supply of beef suet, sometimes supplemented with nuts and twice with an orally injected drop of cod liver oil. On experimental days the bird was allowed to feed for about 0.5 hour after emerging from its roost cavity which occurred about 0.5 hour after dawn. After *ad libidum* feeding the suet bag was removed and the bird fasted for about an hour before being tested. Goldenrod stems with a gall were inserted in holes in a board suspended from the cage ceiling. The stems with galls used on any one date were randomly selected from a large group of galls picked in late fall from one field. Usually two consecutive sets of eight galls each were rapidly attacked by the woodpecker. Observations were made from inside my home (JC) through a window about seven m from the cage. Each hole was numbered, and movement on/off each gall was described into a tape recorder with the elapsed time transcribed later. The contents of each gall were examined after the trial. We used the descriptions of Uhler (1961) to determine if the gall had contained a fly larva or one of the predacious insects, *Eurytoma obtusiventris, Eurytoma gigantea,* or *Mordellistena unicolor* from the condition of the cavity. The average fly larva weight (0.041 g) exceeded that of the predators, all of similar size (0.005 g), by about 8-fold.

Terms and definitions used for this study follow. *Attack initiated:* bird landed on stem, moved up to gall and pecked at gall surface. The bird occasionally would land on a stem without pecking at a gall, which was not counted as a feeding event. *Abandoned:* bird left gall after only pecking at the surface. *Chisel new hole:* bird made a new hole that reached the central cavity of the gall. *Enlarge exit tunnel:* bird located the exit tunnel prepared by the fly larva and enlarged this slightly. *Success:* extraction of a larva was assumed when no larva was found in the gall after the Downy chiseled a hole and the cavity was not completely occluded with resin as occurs if a larva dies during the plant's growing season. *Time:* measured in seconds, was the sum of all time at a gall; it occasionally included repeated visits. *Reward rate:* the weight of insects obtained by a specified feeding behavior prorated to 1 hour, and expressed as a percentage of the Downy Woodpecker body weight of 28 g.

Results

Usually the woodpecker would begin foraging on the galls within seconds of the time the observer backed away from the cage. Occasionally data would be obtained on 16 galls in barely more than a 0.5 hour. Thus, these data may resemble foraging behavior of a hungry Downy Woodpecker in the field, but some influence of confinement is probable.

The woodpecker pecked downward or horizontally so that it had access to the upper half and midline of the gall, which usually included the area with the exit tunnel. The exit tunnel underlies about 1-2% of the searched plant surface, yet 30% of all fly larva extracted by the caged woodpecker were obtained through the exit tunnel, compared to 53% in field surveys (Confer and Paicos 1985). Frequent use of the small entrance to the tunnel, which is covered by plant epidermal cells, implies that the Downy Woodpecker searches for the exit tunnel. Searching is implied also by the bird's initial behavior at a gall. The woodpecker tapped at all accessible portions of the gall by stretching its neck. If the bird did not begin to strike strongly while at its first location on the gall, the bird would move its feet around the gall midline and tap at all newly accessible portions of the gall. This repositioning sometimes occurred 2-4 times before the bird struck strongly enough that chips of the gall were torn away.

Table 1. Predation on goldenrod gall insects by a caged Downy Woodpecker. Numbers represent frequency of occurrence or calculated values as defined in text.

	Fly Larvae			Other Larvae		Sum
	All	Exit	New Hole	All	New Hole	
No. Initiated	106			110		216
No. Abandoned	6			17		23
No. New Hole or Enlarged Exit		30	70		93	193
Percent Success	92	100	97	43	52	75
Mean Time (s)	101	51	131	64	75	84
Reward Rate (%/h)	4.8	10.3	3.9	0.43	0.50	2.6

The frequency of abandonment (Table 1) was low but was significantly greater (Chi-square = 5.74, $p < 0.05$) with galls containing the predacious insects (16%) than with galls containing the fly (6%). Field surveys showed a similar, 3-fold difference in the ratio of these percentages, but the absolute rate was twice as great (Confer and Paicos 1985). The caged woodpecker never abandoned a gall if the epidermal cells over the exit tunnel were punctured (30 galls). If the woodpecker failed to locate an exit tunnel (186 galls), then 12% were abandoned. The time spent on galls that were abandoned was brief; less than 10 seconds on 14 galls, less than 20 seconds on an additional six galls and less than 30 seconds on three other galls.

By far the greatest reward rate, 10% of the body weight per hour, occurred when a fly larva was extracted through the exit tunnel (Table 1). The time required was short, the success was 100%, and the reward is large. Chiseling a hole in a fly gall required considerably more time than enlarging the pre-existing tunnel (Table 1), and had a slightly lower success rate with a resultant reward rate of 4%. Reward rates from the other insects were considerably lower, 0.43%. This low reward rate results both from the lesser weight of the predacious insects and also from the lower success in extracting the larva from the frequently occluded cavity (Table 1).

When the Downy chiseled a new hole, he behaved differently when on galls with fly larva than when on galls containing the smaller insects. The woodpecker spent 131 seconds (standard error = 5.0) chiseling a new hole into a gall with a fly but spent only 75 seconds (standard error = 3.4) on a gall with predacious insects. The lower success of extracting predacious insects compared to the fly probably is due, in part, to the reduced effort. In addition, resin frequently occluded the center of the cavity containing predacious insects. In some instances inspection of the cavity after the woodpecker was done suggested that even a major effort would not have enabled the woodpecker to extract the larva. The central cavity of a gall containing a fly larva always is completely open and the success rate for extracting the larva is very high (97%). Thus, the longer time which a woodpecker takes to extract the fly larva is balanced by the larger reward and a nearly perfect success, resulting in a reward rate of 3.9% (Table 1). The woodpecker abandons the other insects sooner, perhaps because the potential reward is smaller and because failure to extract the insect is inevitable for many galls despite any amount of effort. This minimizes further, possibly fruitless effort. The result is a reward rate of 0.5% (Table 1).

Implications

Previous field data (Confer and Paicos 1985) showed that Downy Woodpeckers frequently abandoned galls when the exit tunnel wasn't located. This abandonment improves the rate of obtaining food because chiseling a hole takes much more time and often results in obtaining either the small predacious insects or nothing at all. On the other hand, the caged bird showed considerably more persistence than was shown by the field data. He usually chiseled a new hole even in galls with the smaller insects. Consequently, he obtained lower reward rate than he would have if he had frequently abandoned galls when the exit tunnel was not located. Our caged bird, which seemed to act hungry, adapted a strategy which yielded a high percentage of the available food. Perhaps Downy Woodpeckers optimize for maximum rate of reward in the field when many galls are available and for maximum amount of reward in the cage when only 8 galls were available at a time.

Lima (1984) demonstrated that Downy Woodpeckers learned to change foraging strategy in a way that enhanced the reward rate as the distribution of an artificial food resource was changed. This study showed three foraging features that enhanced the reward rate and may be learned: the search for the exit tunnel; the higher rate of abandonment of galls lacking an exit tunnel than the rate for galls with the large fly (even though the overall rate of abandonment was low); and the greater time spent chiseling a new hole in fly galls compared to predacious-insect galls. Studies with young, naive Downy Woodpeckers might reveal if these behaviors are inate, or transferred from some other experience, or learned by feeding on goldenrod galls.

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