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CATERPILLAR LEAF DAMAGE, AND THE GAME OF HIDE-AND-SEEK WITH BIRDS¹

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Abstract. In an aviary, field-captured Black-capped Chickadees, *Parus atricapillus*, learned to forage preferentially at trees with either artificially or caterpillar-damaged leaves. The birds also distinguished between species of broad-leaved trees. These individuals showed differences in foraging behavior, possibly related to previous conditioning in the field. When captured, two of the birds were already using leaf morphology (rolls and discoloration) to search for caterpillars. Two others initially disregarded leaf morphology and instead scanned for prey directly. However, when the potential prey was highly cryptic or hidden, the birds all learned to use both tree species and leaf damage simultaneously as cues in their searching effort for specific prey. Caterpillars that were palatable to the chickadees had feeding behaviors that tended to minimize their apparent feeding damage on leaves, while caterpillars that were not eaten did not have these behaviors.

Key words: bird predation; caterpillars; chickadees; cryptic; foraging; herbivory; leaf damage; *Parus atricapillus*; plant-insect interaction; search images.

INTRODUCTION

Many birds of the northeastern United States forests prey heavily on leaf-feeding caterpillars that are highly cryptic (Holmes et al. 1979). However, on broad-leaved trees, caterpillars leave clues to their presence by the leaf damage from their feeding (Thurston and Prachuabmoh 1971). Many such caterpillars, especially those prized by birds, have behavior that tends to reduce the apparent leaf damage (Heinrich 1979). Using Black-capped Chickadees (*Parus atricapillus*), we here test the hypothesis that leaf damage serves as a feeding cue in the birds' search for highly cryptic prey.

THE BIRDS: MATERIALS AND METHODS

All the birds we used were adult males (they sang) and were captured during the breeding season (June and July 1981). They were mist netted and immediately transferred to a nylon-screened holding enclosure (3.7 × 7.4 m and up to 2.4 m high in the center) that contained naturally growing small balsam fir (*Abies balsamea*), spiraea (*Spiraea latifolia*), sprouting red maples (*Acer rubrum*), and numerous dried, dead branches. The enclosure was located in partial shade in a secondary forest of white pine (*Pinus strobus*), birch, and maple near Weld, Maine, where the birds were captured. One end of the holding enclosure was adjacent to a second enclosure of the same size, used for training and testing the birds. Opening and closing flaps between the two enclosures allowed us to trans-

fer a bird between them. We worked with only one bird at a time, except in one case when we transferred a mated pair and the stump containing their nest with five young into the holding enclosure.

We established an artificial deciduous "forest" in the training and testing enclosure by placing 1–2 m tall tops or vertical branches of white birch (*Betula papyrifera*) and/or chokecherry (*Prunus virginiana*) trees in two rows of five trees with 700–1100 fresh green leaves per tree. In some experiments, where indicated, we also used other tree species. We attempted to remove all naturally occurring insects from the trees, but our proficiency at this task, as revealed by the chickadees, was initially poor. In addition, the ground of the training enclosure was covered with plastic sheeting (except when indicated) to prevent birds from foraging on the ground. In some of the experiments, all leaves on 2 of the 10 trees were perforated with 2–15 holes 6 mm in diameter, using a paper punch. All trees with damaged leaves, whether chewed by caterpillars or perforated by paper punch, are herewith designated as the *experimental* trees. Segments of wild rose (*Rosa* spp.) twigs were tied on all 10 trees. During training of the chickadees 5–15 halves of mealworm (*Tenebrio molitor*) were impaled on the thorns of each of the rose twigs on the two experimental trees. To prevent the birds from learning to feed at specific locations (Alcock 1973), trees were moved randomly among the 10 possible locations between foraging bouts. In other experiments we used cryptic caterpillars as prey. The caterpillars were released directly onto the leaves of experimental trees that had natural leaf damage, as found in the field near our enclosure at that time.

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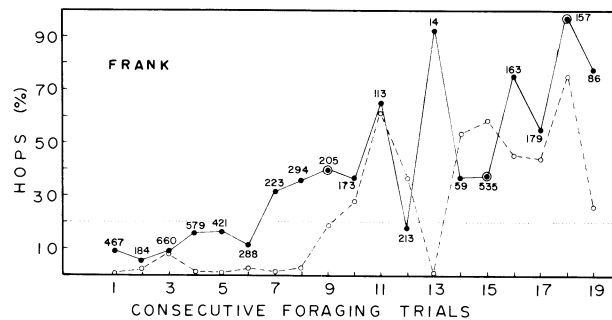


FIG. 1. The percent of hops on the experimental birch trees with damaged leaves and with mealworms (—) and hops on the ground onto which mealworms had fallen (---) by the chickadee named "Frank," over 19 consecutive foraging trials in an aviary. Dotted line indicates expected random visitation among the 10 trees (2 experimental and 8 control without leaf damage and mealworms) in the foraging enclosure. The number of hops for each foraging trial (Figs. 1–5) is indicated with each data point for hops on trees. In trials 9, 15, and 18 (circled) there were no mealworms on any of the trees. In trial 12 the two experimental trees had the damage restricted to only one branch, while >90% of the same trees had whole leaves. Total number of hops during 19 consecutive foraging trials = 5013. Equation of percent hops on experimental trees with reward (y), as a function of foraging trial number (x): $y = -3.40 + 4.78x$, ($r^2 = .66$, $F = 27.1$, $P < .005$). All of the percent hops on experimental trees except those of trials 3, 5, 12, and 14 are significantly ($P < .001$) different from expected random visitation.

We allowed newly captured birds to become accustomed to the holding enclosure (for a few hours to a day) until they were foraging for mealworms conspicuously impaled on rose thorns among dead branches. Food was then withheld for 2–3 h, and the bird was transferred to the training enclosure. After several trials, some of the birds waited at the door and flew into the training enclosure as soon as we lifted the flap. The birds foraged throughout the whole enclosure. We did not observe them to prefer one area (such as the trees near the entrance) over any other. While the bird was foraging, we recorded the number of hops on the ground and on each of the 10 trees. We did not use time spent on the different trees as a measure of preference because the birds often found a food item on one tree and then perched on another to eat it. Although the birds would forage while we were in the enclosure, we made all observations from the outside. We interspersed feeding trials with test trials in which no reward was given, enabling us to determine if the birds were using leaf damage as a foraging cue or were searching for prey directly. All trees were replaced daily and between test trials to prevent birds from recognizing individual trees. The length of each trial (time a bird was maintained in the experimental enclosure) was a function of the time the bird required to feed. Initially, a bird sometimes fed for an hour or more before it went to sleep, bathed, stopped to preen, cached the prey, or switched from hopping among the trees to persistent hopping on the sides of the enclosure.

All of our chickadees began foraging in the enclosure within minutes or several hours. Testing began within a day of capture.

We used χ^2 as our statistical test between expected and observed hopping frequencies. Linear regression

was used to compare means of consecutive foraging trials.

RESULTS

Different individuals appeared to have different foraging techniques, and we therefore describe the results separately.

A mated pair.—On 22 June, we captured a pair of birds at the nest, and transferred them, along with their nest cavity containing five young nearly ready to fledge, into the holding enclosure. The young called for food within minutes, and the adults fed them mealworms we skewered onto brambles near the nest hole. Within an hour both birds were foraging for mealworms and feeding the nestlings until they were silent.

The next day we allowed both birds into the foraging enclosure. They began to forage on the 10 birch "trees" immediately, showing a highly significant ($P < .001$) preference (averaging 30.3 and 48.5% above random visitation in three and five foraging trips for the two birds, respectively) for the two experimental trees with damaged leaves and mealworms.

At that time (23 June) birds in the field were apparently not feeding heavily on caterpillars, and leaf damage from caterpillars was small. Before capturing these birds we watched the nest for 2 h; the adults fed the young 14 large moth abdomens, two small caterpillars, and four unidentified insects.

"Frank."—This bird was captured on 16 June and used for numerous consecutive foraging trials from 16 to 21 June. Frank initially foraged extensively on the floor of the enclosure, which interfered with our efforts to evaluate foraging behavior in trees.

In the first three trials, Frank visited the experimental trees at frequencies ranging from 5.9 to 9.2% (Fig. 1), significantly less ($P < .001$) than the 20% ex-

pected merely by random hopping. He examined leaves closely, hanging upside down from them, picking at them, and opening leaf rolls containing caterpillars. Since there were more leaf rolls on the control trees that did not have damaged leaves than on the experimental trees, we were occasionally rewarding him not only with mealworms that had fallen onto the ground, but also with small caterpillars in leaf rolls on control trees. Nonetheless, after six trials Frank showed a significant ($P < .001$) preference for mealworms in the experimental trees, while continuing to increase his foraging on the ground (Fig. 1). After 10 feeding trials, the bird spent $\approx 50\%$ of his foraging effort on the ground, but when foraging in the trees he showed a significant preference ($P < .001$) for experimental trees (Fig. 1).

Even though Frank foraged by examining leaves closely, the possibility remained that he flew to trees with damaged leaves not because he saw leaf damage, but because he saw the prey itself. However, in three trials (number 9, 15, and 18) when there was no prey on the trees with damaged leaves, the bird visited these trees at a significantly ($P < .001$) greater frequency than expected by random visitation, indicating that he did not favor the experimental trees because he sighted the prey itself. Indeed, the highest percentage of hops (97%) on trees with damaged leaves was recorded on one of these trials (number 18).

"Ralph."—Ralph was captured on 2 July and tested between 2 and 9 July. This bird inspected leaves closely from the first time he foraged in the enclosure, as did Frank. He appeared to specialize on leafmining caterpillars. We found these tiny caterpillars only after we tore open leaves with brown stains in the mesophyll. Ralph, however, did not forage on the ground, since in this and later series we covered the ground with plastic sheets and removed all prey that fell on them before the trial.

After 11 feeding trials Ralph, like Frank, allocated 50% or more of his hops to the trees with damaged leaves (Fig. 2). Both Ralph and Frank showed an ini-

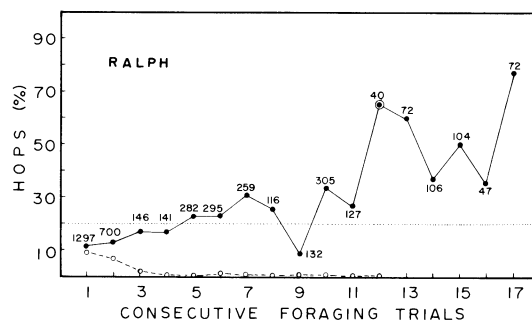


FIG. 2. Foraging performance of chickadee "Ralph." Notation of lines and data points as in Fig. 1. Total number of hops = 4241. Equation of percent hops on experimental trees with rewards (y), as a function of foraging trial number (x): $y = 4.6 + 2.09x$ ($r^2 = .63$, $F = 23.5$, $P < .005$). The percent of hops on experimental trees during trials 1, 2, 7, 8, 9, 12, 13, 14, 15, and 17 are significantly ($P < .001$) different from random expectation.

tial significant ($P < .001$) preference for trees with entire leaves, compared to those with artificially damaged leaves. In later trials they showed a significant preference ($P < .005$) for the experimental trees. Ralph's initial preference for the trees with undamaged leaves may have been related to his search for leafminers, since we discarded most damaged leaves (including those with leafminers) from the experimental trees.

Except in the last trial, number 17 (Fig. 2), Ralph preferred the experimental trees even when they contained no food reward. The food itself was therefore not the immediate visual cue.

"Fernald."—Fern, who was captured 26 June and tested from 26 June to 2 July, did little hopping or inspecting of leaves at close range. Rather, he scanned from a distance and then flew directly to trees with damaged leaves (and the mealworms). In the first trials Fern concentrated well over 50% of his hops in the two experimental trees ($P < .001$), and there was no significant change in this preference as long as the experimental trees contained food (Fig. 3).

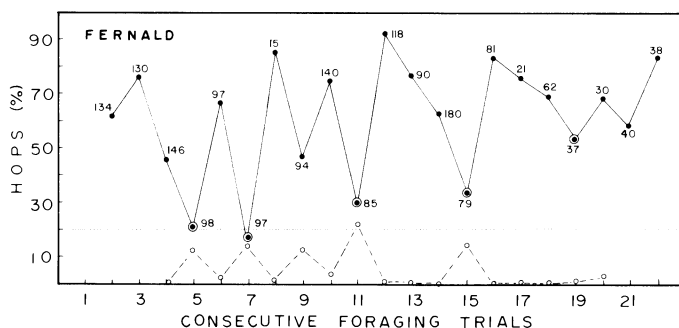


FIG. 3. Foraging performance of chickadee "Fernald." Notation of lines and data points as in Fig. 1. Total number of hops = 1802. Equation of percent hops on experimental trees with rewards (y), as a function of foraging trial number (x): $y = 47.7 + 1.90x$ ($r^2 = .20$, $F = 3.44$, $P > .05$). All the percent hops on experimental trees except those of trials 5, 7, 8, and 11 are significantly different from random expectation.

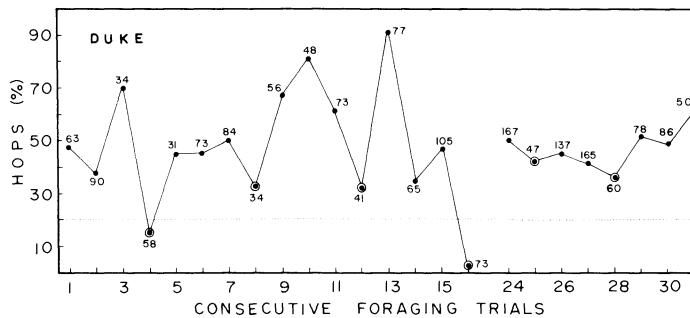


FIG. 4. Foraging performance of "Duke." Notation of lines and data points as in Figs. 1–3. Total number of hops for the 31 foraging trials = 2934. In trial 16 the damaged leaves were on red maple. (The other trees were birch, as before.) In trials 24–31 the mealworms were attached to four (rather than one) small rose twigs hidden among the foliage of the two birches with damaged leaves. Equation for regression of percent hops on experimental trees with rewards (y), as a function of foraging trial number (x): $y = 50.8 + 0.54x$ ($r^2 = .12$, $F = 4.10$, $P > .05$). On the other hand, the equation for regression of percent hops on experimental trees without rewards (y , this figure and Fig. 5) as a function of foraging trial number (x) is: $y = 16.05 + 4.92x$ ($r^2 = .48$, $F = 8.13$, $P > .05$). All the percent hops on experimental trees except those of trials 4, 8, 12, 14, and 15 are significantly ($P < .001$) different from random expectation.

Fern's behavior was also markedly different from that of the previous two birds when we removed the food from the experimental trees. His visitation of experimental trees was initially (trials number 5, 7, and 11) not different from random expectation ($P > .05$). He favored trees with damaged leaves only when they contained prey, indicating that he did not use damaged leaves as a signal but searched directly for mealworms. Eventually, however, Fern also used leaf damage as a cue in searching. In later trials (numbers 15 and 19) he preferred ($P < .01$ and $P < .001$) the trees with damaged leaves but no prey (Fig. 3). In addition, he chose ($P < .001$) trees with damaged leaves when this damage was restricted to only one branch (trials 17–20, Fig. 3).

The change in Fern's behavior is apparent also from his initial tree choices and his giving-up times at experimental trees without food. On foraging trials number 5 and 7 when no food was present (Fig. 3), he made no more than three hops per tree before moving, changing trees 20 and 8 times, respectively, before finding an experimental tree. On the 11th, 15th, and 19th trials, however (Fig. 3), he still made only three hops on each control tree but up to six hops on each experimental tree. In trials 11, 15, and 19 he either flew directly to the experimental trees, or hopped on only three other trees before moving to an experimental tree. Fern learned to search at trees with damaged leaves after only ≈ 15 foraging trials. Before using leaf damage as a cue he seemed to look directly for worms.

"Duke."—Duke² was captured 14 July and tested from 14 to 28 July. As did Fernald, this bird scanned

directly for prey from a distance. In the first feeding trials he spent a significant ($P < .001$) proportion of his hops at the experimental trees; this effort remained high but did not increase ($P > .05$) with subsequent trials (Fig. 4). Furthermore, in trials 4, 8, and 12, when we provided no mealworms, the bird did not visit the experimental trees above random expectation ($P > .05$). These results indicate that he searched directly for mealworms. That Duke was not using leaf damage as a cue also became evident when we tested him on a red maple tree rather than a birch (trial number 16, Fig. 4). The maple tree, although having experimentally damaged leaves, was visited significantly ($P < .001$) less than expected by chance.

Duke probably began to use leaf damage as a cue when his intended prey, the mealworms, became less conspicuous. We made mealworms less conspicuous by hiding them in the foliage on four small rose twigs (rather than leaving them on one large twig). Following this treatment the bird allocated significantly ($P < .001$) more effort to the experimental trees than to the control trees, regardless of whether or not they contained mealworms (trials 24–31, Fig. 4).

Most palatable foliage caterpillars are considerably more cryptic than mealworms. Leaf damage might thus be an even more important cue than our experiments with mealworms had indicated.

In order to test the relationship between "search image" hunting cues and intermediate cues (such as leaf damage and tree species), we conducted tests with highly cryptic prey on naturally damaged trees. We first used naturally damaged chokecherry trees collected near the enclosure. Most leaf damage on this tree species was caused by small, highly cryptic, green geometrid caterpillars (≈ 1 cm long, weighing up to 16 mg) that mimicked the petioles, rachis, and edges of leaves. Each experimental tree was enriched with 40–50 of these caterpillars for a feeding trial. Duke showed

² Motion pictures of Duke foraging can be seen in the NOVA production *The Imposters*, available from Time-Life Distribution Center, 100 Eisenhower Drive, P.O. Box 644, Paramus, New Jersey 07652 USA.

an almost immediate, significant ($P < .001$) preference in searching on such trees (Fig. 5A). Furthermore, after less than three feeding trials he began to show the same preference for the naturally damaged trees, whether or not the caterpillars were actually present (Fig. 5A, trials 35 and 38).

Feeding behavior also changed markedly in other ways after we began to reward Duke with small geometrid larvae. After finding some of these caterpillars, he began to inspect leaves and twigs closely. He pecked at twigs, leaf edges, and leaf irregularities, sometimes tearing the leaves.

In addition to the small geometrid larvae (of which Duke ate 24–30 in any one feeding trial), green heterocampid (Notodontidae) larvae (of which he could only eat two to three at one trial) were also used in feeding trials. The much larger (500–600 mg) notodontid larvae, although they mimicked leaf edges, were to us considerably more conspicuous than the geometrids. After Duke found the first notodontid larvae he seemed to search again by scanning, as he had done with mealworms. In the tests with no caterpillars (numbers 40 and 43) following trials with heterocampids, his preference for experimental trees declined (Fig. 5B). A significant ($P < .001$) preference for trees with leaf damage (Fig. 5B, Trials 39–44) was nevertheless maintained.

Duke was attentive not only to leaf damage, but also to the kind of trees. When eight trees of different kinds, with both damaged and undamaged leaves, were substituted for the eight undamaged chokecherry trees, his preference was unchanged. Duke continued to show a significant preference ($P < .001$) for caterpillar-damaged chokecherry trees over naturally damaged alder (*Alnus rugosa*), undamaged chokecherry, aspen, fir, and pine (Fig. 5C, Trials 45–48).

We continued to test Duke's discrimination ability by providing him with naturally damaged trees of chokecherry, white birch, red maple, alder, and willow (*Salix discolor*). Some of these trees are similar in leaf shape (Fig. 6) and general form. Nevertheless, Duke, who had been foraging for the small green geometrid larvae on damaged chokecherry, was not deceived. When we introduced other species, he continued to fly directly to the chokecherry when let into the feeding enclosure. The results indicate that Duke used both leaf damage and tree species as intermediate cues in his search for cryptic prey.

When a bird entered the foraging enclosure, it sometimes selected a tree with damaged leaves by chance alone. However, with increasing experience (several consecutive trials) there was a highly significant trend ($P < .005$) for all birds to begin searching for food on the experimental trees (Fig. 7). This suggests that the birds recognized leaf damage from a distance.

CATERPILLARS

If the ability of birds to use leaf damage as a foraging cue is general, then caterpillars that are palatable to

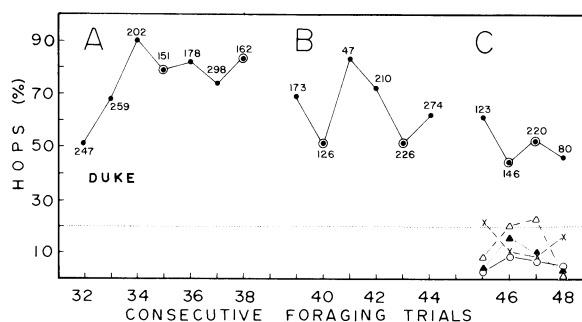


FIG. 5. Foraging performance of "Duke" on caterpillar-damaged (experimental) vs. "clean" (control) chokecherry trees. Notation of lines and data points (in A and B) as in Figs. 1–4. In A the experimental trees contained small highly cryptic geometrid larvae. In B the experimental trees contained large less cryptic heterocampid (Notodontidae) larvae in addition to the geometrids. In C the reward on the two damaged chokecherry trees (trials 45 and 48) was as in B, but the eight control trees, instead of being only undamaged chokecherry (\times), also included naturally damaged alder (Δ), fir and pine (\blacktriangle), and undamaged aspen (\circ). Total number of hops for all trials indicated = 3022. All of the percent hops on experimental trees are significantly ($P < .001$) different from random expectation.

birds should exhibit behaviors that reduce apparent leaf damage. Those that are not palatable to birds (but still influenced by factors such as other predators, parasitoids, and plant defenses) should not exhibit these behaviors. To test this coevolutionary hypothesis is beyond the scope of this paper, inasmuch as it relates to hundreds of bird species and thousands of caterpillar species. Nevertheless, we shall examine various aspects of caterpillar feeding behavior to determine whether or not the hypothesis is supported.

METHODS

Our assessment of the palatability of caterpillars (to chickadees) is based on observations both in the field near the enclosure and in the enclosure itself. We classified caterpillars that the birds ate as "palatable," and those that they did not take when offered in conspicuous fashion (as from our hand) as "unpalatable."

Observations on caterpillar feeding behavior were compiled from several sources. Some caterpillars were placed on low trees, where they were watched in the field. Others were placed on cut trees or branches placed in containers of water. Leaf-clipping behavior was either observed directly or inferred from the appearance of partially eaten leaves with severed petioles on drop cloths or cleared ground directly beneath feeding sites.

Although most of the observations were made in Maine, during July and August 1981, many of those in Table 1 were collected by B. Heinrich over several years in other areas of Maine, Minnesota (Heinrich 1979), and California (Heinrich 1971).

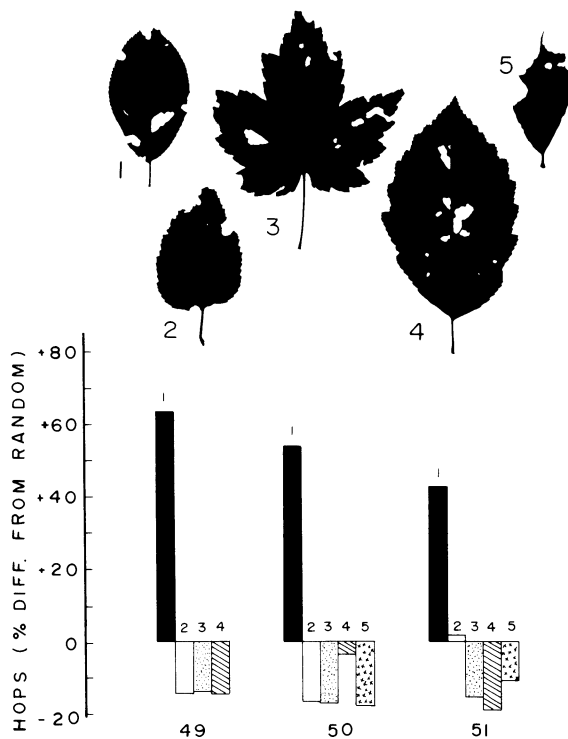


FIG. 6. Tree choice of "Duke" in percent hops different from random expectation on chokecherry trees with naturally damaged leaves vs. four other kinds of trees that also had naturally damaged leaves. The bird had previously been trained to damaged birch (Fig. 4) and chokecherry trees (Fig. 5). The leaf-damaged chokecherry trees contained small cryptic geometrid larvae in trials 49 and 50, but in trial 51 none of the trees contained food reward. 1 = chokecherry, 2 = white birch, 3 = red maple, 4 = alder, 5 = willow. Total numbers of hops in the three trials are 284, 262, and 87, respectively. In all three trials the percent hops on the experimental trees was significantly different ($P < .001$) from random expectation.

Caterpillar palatability

The chickadees accepted without hesitation the smooth-skinned cryptic caterpillars of the heterocampids, geometrids, and sphingids. Large specimens of the saturniid larva *Telea polyphemus* used defensive maneuvers such as cracking their mandibles, swinging their bodies violently, and regurgitating partially digested leaf juices onto attacking birds. These caterpillars were sometimes killed but usually were not eaten even though they were relatively smooth and cryptic. Small individuals of this species were dismembered and eaten, however.

Brightly colored hairy, bristly, or spiny caterpillars (such as the tussock moth caterpillar, *Hemerocampa leucostigma*, most arctiids, including *Halysidota maculata*, the mourning cloak butterflies *Nymphalis antiopa*, or the saturniid moth *Anisota rubicunda*) were not pecked at, even when they walked directly in front

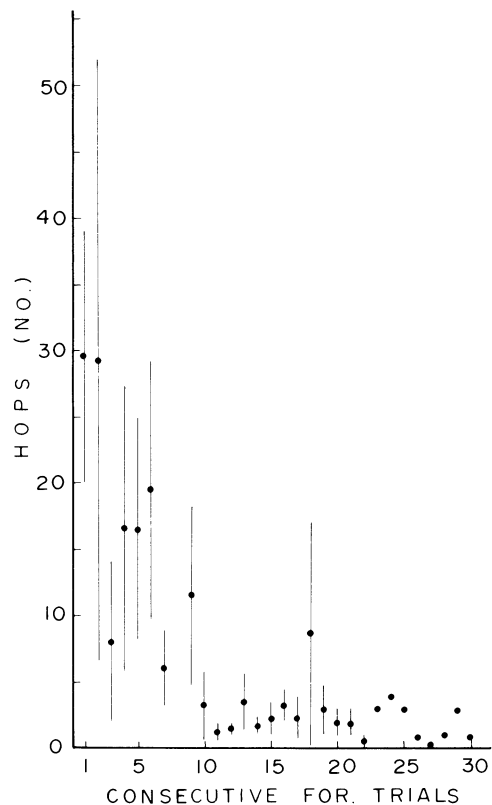


FIG. 7. The number of hops before each chickadee landed on one of the 2 experimental trees (damaged leaves) out of the total of 10 trees. Values are means \pm SE. The number of trials varied from 4 (values at left) to 1 (points at right). Equation for regression of the means (y) on foraging trial number (x): $y = 25.6 - 2.32x + .05x^2$ ($r^2 = .73$, $F = 35.0$, $P < .005$).

of the birds. The chickadees occasionally ate sawfly larvae (Hymenoptera), but only when palatable caterpillars were not available.

When they were hungry and there was no alternative prey, chickadees also accepted caterpillars with silky plumose hair (such as dagger moth larvae, *Acronicta*) but ate only the internal organs, rejecting the skin. Caterpillars of *Zale* sp., which have hairs aiding in counter-shading, were handled similarly.

Leaf damage and caterpillar prey

Of the 40 species for which we were able to gather information (Table 1), 30 fed on trees and 10 (including 6 sphingids) on vines, shrubs, and herbs. Only one of the 10 non-tree feeders (*Sphinx abbotti* on grape) discarded partially eaten leaves by chewing through the petiole, and this species did it only occasionally. Nevertheless, six of the cryptic non-tree species tended to reduce apparent leaf damage by trimming leaves, while the four spiny and/or aposematically colored (and presumably nonpalatable) species usually did not finish leaves, leaving tatters instead (Table 1, Fig. 8).

TABLE 1. Feeding behaviors of species of caterpillars that are cryptic or have plumose hairs ("palatable"), or are aposematically colored, spiny, and/or bristly ("unpalatable," designated with asterisk). Handling of leaves: trimming leaves (+) or leaving tatters (-). Treatment of remnants: eating whole leaf (0), chewing off partially eaten leaves (+), or leaving partially eaten leaves on the plant (-). Data derived from observations of this study and from Heinrich (1971, 1979).

Last-instar caterpillars	Handling of leaves	Treatment of remnants	Food plant examined
Sphingidae (on trees)			
<i>Sphinx chersis</i> Hübner	+	0 +	<i>Fraxinus</i>
<i>Sphinx kalmiae</i> Smith & Abbott	+	0 +	<i>Fraxinus</i>
<i>Ceratomia undulosa</i> (Walker)	+	0 +	<i>Fraxinus</i>
<i>Smerinthus jamaicensis</i> Drury	+	0 +	<i>Populus</i>
<i>Paonia excaecatus</i> Smith & Abbott	+	0 +	<i>Salix</i>
<i>Paonia myops</i> Smith & Abbott	+	0 + -	<i>Prunus</i>
<i>Pachysphinx modesta</i> Harris	+	+	<i>Populus, Salix</i>
Sphingidae (on shrubs, vines, or herbs)			
<i>Hemaris thisbe</i> (Fabricius)	+	0 -	<i>Viburnum</i>
<i>Darapsa choerilis</i> Cramer	+	0 -	<i>Viburnum</i>
<i>Sphecodina abbotti</i> Swainson	+	+ -	<i>Vitis</i>
<i>Manduca sexta</i> (L.)	+	0 -	<i>Solanum, Datura</i>
<i>Manduca quinquemaculata</i> (Haw.)	+	0 -	<i>Solanum, Datura</i>
<i>Hyles gallii</i> (Rottenburg)	+	0 -	<i>Galium</i>
Saturniidae (on trees)			
<i>Callosoma promethea</i> Drury	+ -	+ -	<i>Fraxinus</i>
* <i>Anisota rubicunda</i> Fabricius	-	-	<i>Acer</i>
<i>Telea polyphemus</i> Cramer	+	0 + -	<i>Acer</i>
<i>Telea polyphemus</i> Cramer	+	0 -	<i>Betula</i>
* <i>Samia cecropia</i> L.	-	-	<i>Fraxinus</i>
Notodontidae (on trees)			
<i>Schizura unicornis</i> Smith & Abbott	+	0 +	<i>Betula</i>
<i>Heterocampa guttivitta</i> (Walker)	+	0 + -	<i>Acer</i>
<i>Heterocampa guttivitta</i> (Walker)	+	0 -	<i>Betula</i>
<i>Heterocampa biundata</i> Walker	+	0 + -	<i>Acer</i>
<i>Heterocampa biundata</i> Walker	+	0 -	<i>Betula</i>
<i>Notodonta stragula</i> Grote	+	0 + -	<i>Salix</i>
<i>Cerura cinerea</i> (Walker)	+	0 + -	<i>Populus</i>
<i>Phaeosia rimosa</i> Packard	+	0 -	<i>Populus</i>
Noctuidae (on trees)			
<i>Zale</i> sp.	+	0 +	<i>Populus</i>
<i>Catocola cerogama</i> Guenée	+	+	<i>Tilia</i>
<i>Catocola relictia</i> Walker	+	0 +	<i>Populus</i>
<i>Acronicta americana</i> Harris	+	+	<i>Acer</i>
<i>Acronicta rubicoma</i> Guenée (?)	+	0 +	<i>Populus</i>
<i>Acronicta leporina</i> (L.)	+	0 +	<i>Populus</i>
Liparidae (on trees)			
* <i>Hemerocampa leucostigma</i> Abbott and Smith	-	-	<i>Prunus</i>
* <i>Dasychira dorsipennata</i> (Barnes)	-	-	<i>Tilia</i>
Lasiocampidae (on trees)			
* <i>Malacosoma disstria</i> Hübner	-	-	<i>Populus, Tilia</i>
* <i>Malacosoma americana</i> Fabricius	-	-	<i>Prunus</i>
Arctiidae			
* <i>Arctia caia</i> L.	-	-	<i>Aster</i>
* <i>Halysidota maculata</i> Harris	-	-	<i>Betula, Acer</i>
Nymphalidae (on trees)			
* <i>Nymphalis antiopa</i> L.	-	-	<i>Salix, Populus</i>
* <i>Nymphalis j-album</i> Boisduval & Leconte	-	-	<i>Ulmus</i>
Daniidae			
* <i>Danaus plexippus</i> L.	-	-	<i>Asclepias</i>
Papilionidae			
* <i>Battus philenor</i> (L.)	-	-	<i>Aristolochia</i>
Nymphalidae			
* <i>Nymphalis milberti</i> Latreille	-	-	<i>Urtica</i>

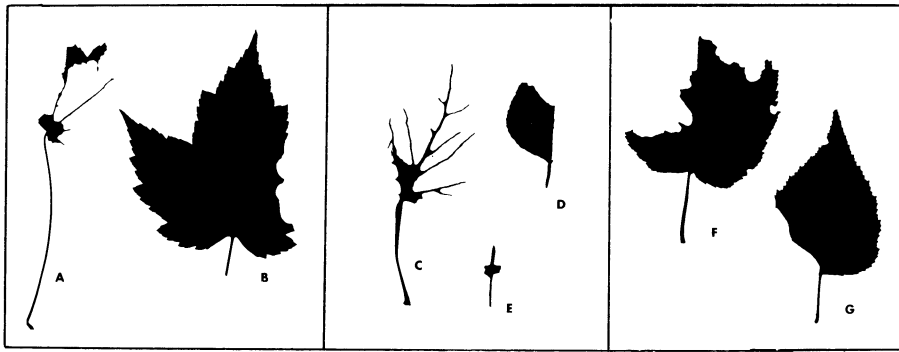


FIG. 8. Representative feeding damage of colorful, hairy, and spiny ("unpalatable") caterpillars (A, C, and F), and nonspiny cryptic ("palatable") caterpillars (B, D, E, and G). A = *Anisota rubicunda* on red maple; B = *Telea polyphemus* on red maple, showing leaf trimming and petiole clipping; C = *Nymphalis antiopa*; D = *Zale* sp., showing leaf trimming and petiole clipping; E = *Acronicta americana*, showing leaf trimming and petiole clipping; F = *Halysidota maculata*; G = *Heterocampa* sp., showing trimming but no clipping.

Of the 30 tree-feeding species, only 9 were spiny and/or aposematically colored (unpalatable). Of these, none was observed to chew off and discard partially eaten leaves. However, of the 21 species that were cryptic or had soft plumose hairs, all but 1 clipped off partially eaten leaves. In addition, all of the latter group tended to trim leaves, while none of the spiny and/or aposematically colored species did so.

"Clean" and "messy" feeders were found on the same kinds of trees. Maple, birch, and trembling aspen (*Populus tremuloides*), for example, each had both types (Table 1). Caterpillar feeding damage could be observed in the field even on individual leaves. However, from a distance, feeding damage was much more conspicuous when damaged leaves were in groups. Nonpalatable caterpillars were often surrounded by leaves damaged by feeding over several instars. In addition, nonpalatable caterpillars (*N. antiopa*, *H. maculata*, *A. rubicunda*) also occurred in groups, amplifying their visibility. The nonpalatable caterpillars ate the choicest parts of the leaves, generally leaving tough portions such as midribs and large veins. None of them was ever observed to chew into a petiole, and all of them fed both day and night.

The cryptic, palatable caterpillars fed either both day and night or only at night, depending on their methods of disguise. In general, caterpillars that were cryptic on leaves or parts of leaves fed both day and night, as they stayed on leaves at all times. Those that were cryptic on twigs or bark fed only at night. Both kinds left little leaf damage because they ate entire leaves, pared leaves down to eliminate holes, chewed off partially eaten leaves at the petiole, or exhibited a combination of these behaviors (Table 1).

All of the cryptic sphinx moth caterpillars chewed leaves cleanly, leaving no leaf tatters (Table 1). The caterpillars of *Poania* and *Smerinthus* (on poplar, cherry, and willow) usually completely consumed the

relatively small leaves of their host plants. On the other hand, sphinx moth caterpillars feeding on trees with large leaves almost always chewed off leaf remnants and/or portions of the petiole after finishing a leaf. Sphinx moth caterpillars feeding on herbs and shrubs did not chew off leaf remnants.

The larvae of *Telea polyphemus* (Saturniidae), which fed both day and night, usually entirely consumed small leaves, such as those of poplar or birch. However, when these larvae fed on large leaves, such as those of maple, they often chewed off unfinished portions before moving. Caterpillars that hid in the daytime and fed only at night (*Catocola* sp. and *Zale* sp.) chewed off partially eaten portions of leaves before resuming their hiding position on branches or tree trunks.

The heterocampid leaf-edge mimics fed both day and night. On birch, they did not usually chew off partially eaten leaves but stayed with a leaf until it was finished or until they were ready to pupate. When feeding on large maple leaves, however, they commonly chewed through the petiole, discarding the uneaten leaf remnant. Thus, there was relatively little visible leaf damage where this highly palatable larvae fed. Still another species, *Schizura unicornis*, mimicked a dead portion of a leaf; it not only ate the entire leaf (birch) but cut the petiole off at the base. Three species of dagger moths on poplar (*Acronicta leporina*, *A. rubicoma*, and *A. americana*) almost invariably chewed off leaf remnants (Table 1). However, one species, *A. americana*, severed the petiole where it joined the twig, not leaving even a petiole where it had fed.

None of the small green geometrid larvae used in the feeding experiments chewed off leaves, and none stayed to finish an entire leaf. Indeed, their small size presumably makes chewing through the relatively thick and tough leaf petiole very slow and difficult. The defensive strategy of these larvae is apparently to move from place to place and to remain hidden. When aligned

along leaf edge, midrib or petiole, these larvae are very inconspicuous, even with close and direct inspection.

Leaf damage and caterpillars in the field

If palatable caterpillars disguise or discard their feeding damage, while nonpalatable caterpillars do not, then one might predict that birds would find no advantage in searching near damaged leaves. On the other hand, different kinds of caterpillars tend to occur together on certain food plants. It might thus be advantageous for a bird to disregard leaf damage on one kind of tree but not on another. We examined the prediction that palatable caterpillars would be associated with at least some leaf damage by walking through the forest and noting the presence or absence of leaf damage and caterpillars by scanning 100 1-m² patches of foliage for 10 s.

The presence or absence of palatable caterpillars was dependent on the tree species (Fig. 9). Most (87%) of our observations for alder, for example, revealed conspicuously damaged leaves, yet only seven caterpillars were noted. Chokecherries were nearly all (97%) heavily damaged (primarily by the small green geometrid larvae we used in feeding trials). However, we found a palatable larva within 10 s of search time in 52% of the foliage patches examined (Fig. 9). Approximately half (45%) of the patches of red maple contained leaf damage, but this damage was primarily associated with the conspicuous spiny larva of *A. rubicunda* that the chickadees avoided. White birch also had a high proportion (56%) of leaf damage, and the caterpillars associated with this damage were mostly (29 out of 41) palatable. The 44 white birch patches where feeding damage was not immediately apparent yielded only four palatable larvae. Thus, although the leaf damage on white birch tended to be inconspicuous and restricted to few leaves, a bird searching near damaged leaves would be at least seven times more likely to find a prey item than one not using leaf damage as a cue.

DISCUSSION

At least two hypotheses on mechanisms of bird foraging for caterpillars could be examined. On the one hand, leaf damage could be a useful cue, because palatable caterpillars are often present at damaged leaves even though they try to hide damage. On the other hand, leaf damage is not a useful cue, because caterpillars quickly move away to avoid chemical defenses mounted by the plant (Carroll and Hoffman 1980). We here show experimentally that leaf damage can indeed be a searching cue to a bird, lending support to the first hypothesis.

Our results show that under seminatural conditions Black-capped Chickadees can use leaf damage as a cue to rewarding food patches when the prey are not visually conspicuous. In our experimental aviary, all four

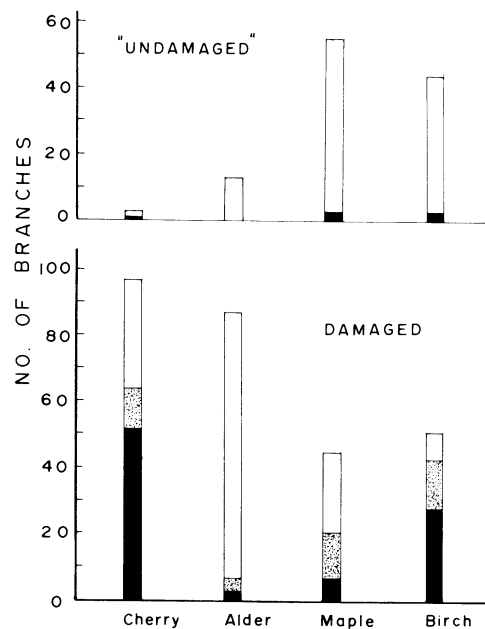


FIG. 9. Number of branches ($\approx 1\text{-m}^2$ area) with damaged leaves (bottom) and "undamaged" leaves (top) out of a sample of 100 branches in each of four tree species on 26 and 27 July 1981. Open bars = no caterpillars visible. Stippled bars = number of branches with one to seven unpalatable caterpillars visible. Solid bars = number of branches with one to three palatable caterpillars visible. Note that (1) most cherries and alders had damaged leaves, and only half of the maples and birches showed leaf damage, and (2) there were 7 times more palatable caterpillars associated with damaged than with undamaged leaf patches of birch.

experimental birds quickly learned to use damaged leaves as a searching cue. The more obvious the prey (determined, in part, by the birds' experience), the less the birds relied on alternate cues such as leaf damage or kind of tree. Parids are well known to show flexible foraging responses, even in laboratory situations (Krebs et al. 1977), and our results indicate that the birds might be even more sophisticated foragers than previously supposed.

Our use of the number of hops at different trees as a preference criterion could underestimate the birds' actual recognition of leaf damage for two reasons. First, two of our birds used the "stop-and-look" foraging technique, and one or two hops may have sufficed for them to determine that a particular tree or branch had no food, causing them to search elsewhere. Second, the number of hops on the different trees was not always a direct function of search effort on these trees, even in the birds that investigated the leaves individually and closely. After finding a caterpillar (particularly a large one) the birds often hopped through several other trees, apparently searching for a suitable perch on which to eat it.

Newly captured birds showed large individual dif-

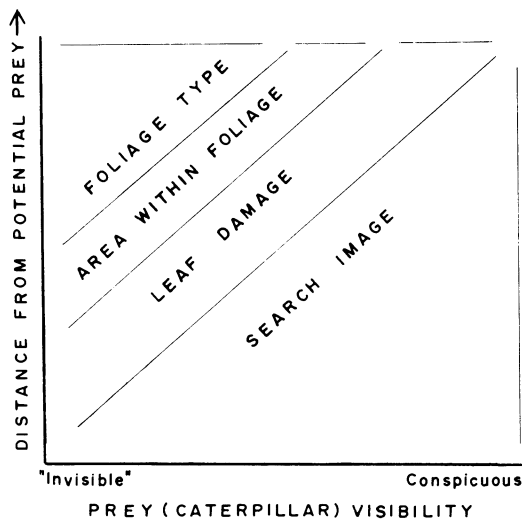


FIG. 10. Model showing possible hierarchy of cues used to localize and locate caterpillar prey on broad-leaved trees as a function of prey visibility. (It is expected that prey visibility to a bird would increase with experience.)

ferences in foraging behavior, and the experimental birds in general exhibited behavioral flexibility during the foraging trials. Two were already using leaf appearance in their search; one sought out stained leaves (which contained leaf miners in the mesophyll), and the other bird opened leaf rolls (some of which contained caterpillars). Both of these birds rapidly learned to use our experimental leaf damage as a foraging cue. The bird that foraged heavily on the ground (before we covered it with plastic sheet) also used leaf damage as a cue when foraging in trees.

In addition to allowing birds to localize their search, recognition of leaf damage should allow an individual to find a broader range of prey than it could by a specific search image. Effective use of leaf damage as a foraging cue, however, requires that birds discriminate accurately among tree species. Our experiments show that the birds can use leaf damage and can recognize the kind of tree. On some trees leaf damage is associated with palatable caterpillars. On others it is associated with noxious caterpillars, and on still others it only means that something has been feeding there in the past.

Leaf damage probably becomes a less reliable cue late in the season as damage on leaves accumulates. In the area of our study in late July, for example, it would have been advantageous for a bird to avoid all alder and red maple, regardless of the amount of leaf damage. On the other hand, even at this time, a bird would have been much more likely to find prey by foraging near damaged birch leaves than near undamaged leaves.

We cannot be sure if minimization of apparent leaf damage by caterpillars has evolved only in response

to avian predators or to other predators and parasitoids as well. We have observed heavy tachinid fly parasitism of mourning cloak caterpillars. These spiny caterpillars are located easily because of conspicuous leaf damage; if parasitic flies use leaf damage cues, these caterpillars should also disguise their feeding damage. However, since all caterpillars are subject to insect parasitism, but only species palatable to birds (particularly those in forest trees) minimize their feeding damage, we suggest that the data are most consistent with the hypothesis that the caterpillar feeding behaviors have evolved under selective pressure of birds, rather than some other agents.

In conclusion, although we have not shown that birds use leaf damage as a foraging cue in the field, our results under seminatural conditions show that Black-capped Chickadees have the ability to do so. We demonstrate further that even though palatable caterpillars disguise apparent feeding damage, or rest at some distance from it, leaf damage is often a reliable cue. For it to be effective, however, birds must also be effective detectives and tree "taxonomists." Chickadees forage from a variety of trees (Brewer 1963), and indirect evidence suggests that they effectively discriminate trees along taxonomic lines; chickadees in a northern hardwood forest foraged preferentially on yellow birch (*Betula allegheniensis*), which contained more potential prey than other available trees (Holmes and Robinson 1981).

We propose a simple, hierarchical model of avian foraging cues (Fig. 10). Search images (Tinbergen 1960, Pietrewicz and Kamil 1979) can only be effective for highly visible prey or for cryptic prey at close range. Birds presumably have innate and/or learned preferences (Klopfer 1965, James 1971) for specific kinds of vegetation (Brewer 1963, Partridge 1976, Holmes and Robinson 1981) and sites (Royama 1970) or areas within the vegetation (MacArthur 1958). After they are near the location where prey is likely to be found (Alcock 1973) they may, as suggested here, use leaf damage to localize their search still further.

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