

**Density-Related Predation by the Carolina Chickadee, *Poecile carolinensis*,
on the Leaf-Mining Moth, *Cameraria hamadryadella*
at Three Spatial Scales**

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ABSTRACT

The impact of predation by the Carolina Chickadee, *Poecile carolinensis*, on populations of the leaf-mining moth, *Cameraria hamadryadella*, was inversely spatially density-dependent at each of three spatial scales: among woodlands, among trees, and among leaves. *P. carolinensis* exhibited an aggregative response to the density of *C. hamadryadella* at the scale of woodlands, but did not preferentially forage in trees or on leaves with high densities of leaf mines. *P. carolinensis* exhibits no numerical response to the abundance of *C. hamadryadella*.

The functional response of *P. carolinensis* suggests that per capita foraging efficiency is actually lower in high-density populations of *C. hamadryadella*. This may arise because of predator confusion and because of mechanical limitations to foraging behavior. Human subjects, used as surrogates for chickadees, took more time to discover and discovered fewer leaf-miner larvae on leaves with higher proportions of the leaf-area mined. Chickadees hang "upside down" to attack leaf-miner larvae and this posture may limit the duration of foraging bouts. Either predator confusion or mechanical limitation, alone or in combination, could account for the observed inversely density-dependent impact of predation at the leaf scale.

In outbreak populations of *C. hamadryadella* where *P. carolinensis* is a common predator, the inversely density-dependent attack by *P. carolinensis* on *C. hamadryadella* complements the strongly density-dependent mortality caused by intra-specific competition. Therefore, the pattern of predation by *P. carolinensis* contributes more to suppression of *C. hamadryadella* than would occur if *P. carolinensis* foraged in a density-dependent manner.

Birds in the family Paridae appear to be the dominant avian predators of leaf-mining insects. We suggest that their altered leg musculature permits them to use a hanging "upside down" posture more frequently and pre-adapts them for foraging on leaf-mining insects feeding on broad leafed plants.

Key Words: *Cameraria hamadryadella*, leaf mining, avian predation, *Quercus*, Carolina Chickadee, *Poecile carolinensis*, Paridae, density-dependence, and foraging behavior.

INTRODUCTION

Birds can impose substantial mortality rates on forest insects (Holmes et al. 1979, Torgersen et al. 1990, Marquis and Whelan 1994), but unless they exhibit either a numerical, functional, or aggregative response to their prey, birds are unlikely to exert any controlling influence on insect populations exhibiting "outbreak" dynamics (Holmes 1990). For insect species that exhibit population outbreaks, outbreaks are usually sustained for only a few years, are restricted geographically, and usually consist of a single insect species. Therefore, a numerical response by avian predators to increased insect abundance is unlikely to occur in the limited space and time over which an outbreak occurs. On the other hand, birds may quickly learn how to find and handle novel prey, and may focus their foraging activity in "profitable areas" (Royama 1970). Hence, avian predators may be expected to exhibit an aggregative and/or a functional response to increases in insect density.

In laboratory experiments, Smith and Dawkins (1971) and Smith and Sweatman (1974) showed that great tits, *Parus major*, exhibited an aggregative response to increasing prey densities in a patchy, albeit artificial, environment. Smith and Sweatman (1974) also found that a higher percentage of prey were removed from high density patches, a density dependent effect that could be due to either an aggregative response, functional response, or both.

Aggregative and/or functional responses by parids have also been documented in field studies (Gibb 1958, 1966, Holmes and Schultz 1988). Gibb (1958, 1966), in his studies of the blue tit (*Parus caeruleus*) and the coal tit (*Parus ater*), showed that individual birds concentrated their feeding in trees with higher densities of larvae of the eucosmid moth (*Ernarmonia conicolana* Heyl.), and that a greater proportion of prey were eaten in trees with high prey density. Holmes and Schultz (1988) found that the Black-capped Chickadee (*Poecile atricapillus*) aggregated its attack on lepidopteran

larvae to leaf petioles and twigs, avoiding leaf surfaces.

Although relatively large lepidopteran larvae make up the greatest proportion of the diet of forest birds, avian predation of the small, late-instar larvae and pupae of leaf-mining insects has also been observed (Itämies and Ojanen 1977a, Heads and Lawton 1983a, Heinrich and Collins 1983, Connor and Beck 1993). Of those studies that examined the spatial pattern of avian predation on leaf-mining insects, one study found mortality to be positively density-dependent and two studies reported inverse density-dependence. Itämies and Ojanen (1977a) examined predation by *Parus major* and *Parus montanus* on *Lithocolletis* (= *Phyllonorycter*) *froelichiella* Z. and *L. strigulatella* Z. and found that predation rates were positively and significantly correlated with the average density of leaf mines in different birch woodlands. Heads and Lawton (1983a) reporting on the mortality caused by *Parus caeruleus* preying on *Phytomyza ilicis* Curtis, and Connor and Beck (1993) reporting on the mortality caused by *Poecile* spp. preying on *Cameraria hamadryadella* Clemens, found avian predation to be inversely density-dependent at small spatial scales.

It is important to insure that the responses of predators to prey density are detected if they are present. Since different prey species may be aggregated at different spatial scales (Heads and Lawton 1983a, Taylor 1984, Cappuccino 1988, Rothman and Darling 1990, Brown *et al.* 1997) and predators may respond differently to prey density at different spatial scales, studies that focus on a single spatial scale may fail to detect the responses of predators to prey density (Heads and Lawton 1983a). For example, Heads and Lawton (1983a) and Connor and Beck (1993) found predator induced mortality of leaf miners to be inversely density dependent at the scale of individual leaves. That is, the proportion of mines preyed upon was inversely related to the number of mines on a leaf. However, Itämies and Ojanen (1977a) found that avian predation was higher in woodlands with high leaf-miner densities. In combination, these results suggest that the response exhibited by avian

predators to prey density may depend on the spatial scale at which predation is studied. Determining the appropriate scale to study may be particularly difficult when considering mobile vertebrate predators preying on sedentary prey species such as leaf miners and gall formers (Hails and Lawton 1983a). It also indicates that studies that simultaneously examine multiple scales may be necessary for a complete understanding of the dynamics of the interactions between predator and prey.

To determine how an avian predator responds to prey density at different spatial scales, the contribution of functional and aggregative responses to prey density in generating the observed pattern of prey mortality, and the potential for avian predation to lead to population declines, we studied the interaction of Carolina Chickadees (*Poecile carolinensis*) and the leaf-mining moth *Cameraria hamadryadella*. The foraging behavior and the pattern of prey mortality caused by *P. carolinensis* was examined at three spatial scales - among leaves, trees, and woodlands.

METHODS

Study Organisms and Study Site

Cameraria hamadryadella Clemens (Lepidoptera: Gracillariidae) is a bivoltine leaf miner that feeds on oak trees (*Quercus* sp.). The life history of *C. hamadryadella* is described in Hinckley (1972), Connor (1991), Connor and Beck (1993), and Connor *et al.* (1994). *C. hamadryadella* usually occurs at low densities, but outbreak populations have been observed (Solomon *et al.* 1980, Connor and Beck 1993, Connor *et al.* 1994, Auerbach *et al.* 1995). Densities reach their highest during the first mining generation, and are also highest in the lower portions of the crown of their host trees (Auerbach *et al.* 1995, Brown *et al.* 1997). Mature first generation larvae and pupae of *C. hamadryadella* are available for attack by avian predators from late June until early August.

Both avian and invertebrate predators attack leaf mines of *C. hamadryadella*. The Carolina Chickadee (*Poecile carolinensis* Audubon) was the only avian species observed foraging on *C.*

hamadryadella at our study sites between 1982 and 1996. The life history and biology of *P. carolinensis* and the closely related *Poecile atricapillus* L. is described by Brewer (1961) and Smith (1991), respectively. Chickadee predation was never observed before mid June when first generation leaf mines begin to expand rapidly in size. Observations were made on avian foraging in July at which time individuals and groups of chickadees were observed. We interpret the presence of foraging groups to indicate that birds were off the nest and at least potentially able to aggregate their attack to areas of high prey density. The hymenopteran predator *Symmorphous canadensis* Sasseur (Hymenoptera: Vespidae) is the only documented invertebrate predator of *C. hamadryadella*, but accounts for a small proportion of predation (Brown *et al.* 1997, and personal observation). A large complex of parasitic hymenoptera also attack *C. hamadryadella* (Connor and Cargain 1994).

All observations were conducted at the University of Virginia's Blandy Experimental Farm in Clarke County, Virginia, USA during the summers of 1994 and 1995. Observations were made at four woodland sites within the farm: the oak grove (1 ha in area) located in the Orland E. White Arboretum, and in three unmanaged woodlands (2.4, 4.8, and 14.4 ha in area) dominated by *Quercus* sp. and *Carya* sp. that lie within 1.5 km of the oak grove. *Cameraria hamadryadella* had previously been observed to pass through population outbreaks and crashes in the oak grove, but not in the other woodlands (Connor and Beck 1993, Connor *et al.* 1994, Auerbach *et al.* 1995). During this study, *C. hamadryadella* was experiencing an outbreak that lasted from 1991-1995. At the peak of the outbreak, population densities of *C. hamadryadella* exceeded 40 mines/leaf in the oak grove, but were much lower in the woodlands (Auerbach *et al.* 1995, Brown *et al.* 1997).

Estimating *C. hamadryadella* Density and Predation by *P. carolinensis*

We estimated the density of *C. hamadryadella* and rate of predation by *P. carolinensis* on *C. hamadryadella* on individual leaves, individual trees, and at four woodland sites. To estimate density

and predation rates on leaves, trees and sites, we randomly sampled three or four *Q. alba* L. trees from each of the four sites in July of 1995 for a total of 20 trees. Three or four branches each with a minimum of 30 leaves were collected at random from the lower crown of each tree. Each leaf was examined and the number of mines of *C. hamadryadella* and the number with predation scars were counted. Leaf mines attacked by *P. carolinensis* have distinct triangular, beak-shaped tears in the leaf mine epidermis. We interpreted these marks to be predation scars although some may represent unsuccessful attacks. Densities were calculated for each woodland site as the average of the number of mines/leaf estimated on each tree, and predation rates were calculated as the average of the proportion of mines preyed upon on each tree.

The estimates of density and predation rate calculated for each tree at each site were used to provide data on the variation among trees in the density of *C. hamadryadella* and the rate of predation by *P. carolinensis*. We also used the data from these samples to estimate the number of mines/leaf and the proportion preyed upon for individual leaves. A total of 543 leaves with leaf mines were collected and individually examined for the twenty trees sampled among the four sites. The number of mines and the proportion preyed upon were recorded for each leaf. We also collected 19 leaves from the oak grove site upon which we directly observed *P. carolinensis* to forage. Each leaf was inspected to determine the number of mines and the proportion preyed upon. We analyzed these data by performing ordinary least squares regression (OLS regression) and, where necessary, non-linear regression (NL regression) of the angularly transformed proportion and the untransformed proportion of mines preyed upon on the number of mines per leaf estimated for sites, trees, and individual leaves. We report only the results of regressions using the untransformed proportion preyed upon because they do not differ from those using the transformed proportions.

Estimating Foraging Investment by *P. carolinensis* among Sites and Trees

To determine if foraging investment by *P. carolinensis* is related to the density of *C. hamadryadella* mines on *Q. alba* at a site, we estimated the abundance of *P. carolinensis* at each of the four study sites in July of 1994 and 1995. At each site, sample points spaced at least 50 m apart were chosen at random within the forest so that the number of points ranged from 3 to 15, depending on the size of the woodland. The number of *P. carolinensis* heard calling in two minutes at each point was recorded and the abundance of *P. carolinensis* at each site was estimated as the average number of individuals heard per sample point. Each sample site was visited a single time each year. We excluded sightings of chickadees from our estimates of abundance because chickadees were more easily observed at some sites than at others. We analyzed these data by performing OLS regressions of the average number of chickadees/sample point at each site on the average number of mines/leaf at each site for both 1994 and 1995.

To determine if foraging of *P. carolinensis* among individual trees was related to the density of *C. hamadryadella* mines on a tree, we followed individuals and groups of foraging *P. carolinensis*, in the oak grove during July of 1994. We recorded the number of individuals and the time spent foraging in each tree, and estimated the density of *C. hamadryadella* mines in each tree. Foraging investment for each tree was estimated as the total number of foraging minutes summed among all *P. carolinensis* individuals that we observed foraging in that tree. The density of *C. hamadryadella* was estimated by removing at random 20 leaves from each tree and inspecting each leaf to determine the average number of mines/leaf on each tree. We observed *P. carolinensis* foraging upon and estimated the density of *C. hamadryadella* on a total of 73 trees comprising several oak species. We analyzed these data by performing an OLS regression of the total number of foraging minutes observed on each tree on the number of mines/leaf estimated for each tree.

To determine if chickadees preferentially attack mines on leaves with high densities, we

compared the densities of *C. hamadryadella* on leaves that had at least one mine attacked by *P. carolinensis* to densities on leaves with no mines attacked. We used trees as our subjects and performed a paired *t* - test ($n = 18$, since on two trees no mines were attacked by *P. carolinensis*).

Leaf and Leaf-mine Characteristics and Chickadee Foraging Decisions

The characteristics of mined leaves might effect foraging decisions among and within leaves by chickadees. We used human subjects as surrogates to determine if the transparency of the leaf mine epidermis, the proportion of leaf area mined, the number of mines/leaf, or the number of mines/cm² of leaf area were related to the rate of discovery of larva of *C. hamadryadella*. After identical initial training, human subjects ($n = 30$) were given a fresh leaf of *Q. alba* with varying numbers of leaf mines with live larvae and instructed to locate and mark as many larvae as possible. We recorded the time required to locate the first larva, and the total number correctly discovered in a period of one minute. We then excised the leaf mine epidermis above each larva discovered and measured the percent transmittance of light through the leaf mine epidermis in the visible spectrum (400 - 700 nm) using a Hitachi 100 - 40 (UV - Visible) spectrophotometer. We performed OLS regressions of the time to discover the first larva and the total number of larvae discovered on: 1) the number of mines/leaf, 2) the number of mines/cm², 3) the proportion of the leaf area mined, 4) the percent transmittance of light through the mine epidermis above the first discovered larva, and 5) the average percent transmittance of light through the epidermis above all discovered larvae.

RESULTS

The abundance of chickadees was directly proportional to the estimated number of *C. hamadryadella* mines/leaf among the four sites in both years, but only statistically significantly so in 1994 (1994: $r = 0.96$, $p = 0.041$, $df = 2$; 1995: $r = 0.56$, $p = 0.44$, $df = 2$, Figure 1). The total foraging time of chickadees observed on individual trees in the oak grove was independent of the

average number of *C. hamadryadella* mines/leaf on each tree ($r = 0.10$, $p = 0.38$, $df = 71$, Figure 2). Furthermore, the average density of mines of *C. hamadryadella* on leaves attacked by *P. carolinensis* did not differ from the densities of *C. hamadryadella* observed on leaves not attacked by *P. carolinensis* (paired $t = 1.375$, $p = 0.188$, $df = 16$).

The time required for human subjects to discover the first larva on a leaf and the number of larvae discovered in one minute was independent of the number of mines/leaf, the number of mines/cm² of leaf area, and the percent transmittance of light by the leaf mine epidermis (Table 1). However, both the time required to discover the first larva and the number of larvae discovered in one minute were related to the proportion of the leaf area mined. On leaves with a greater proportion of their area mined, it took more time to discover the first larva ($r = 0.41$, $p = 0.025$, $df = 28$, Figure 3a), and fewer larvae were discovered ($r = -0.38$, $p = 0.04$, $df = 28$), Figure 3b).

The proportion of mines preyed upon was inversely proportional to the number of mines/leaf when examined for woodlands (OLS regression, $r = -0.98$, $p = 0.018$, $df = 2$, Figure 4a), trees (OLS regression $r = -0.37$, $p = 0.11$, $df = 18$, NL regression, $R^2 = 0.15059$, Figure 4b), and individual leaves (OLS regression $r = -0.19$, $p < 0.0001$, $df = 541$, NL regression $R^2 = 0.0971$, $df = 541$, Figure 4c). For those leaves we observed chickadees to forage upon, the proportion of mines preyed on was also inversely proportional to the number of mines/leaf (OLS regression $r = -0.49$, $p = 0.034$, $df = 17$, Figure 4d).

DISCUSSION

The higher abundance of *P. carolinensis* on sites with higher density populations of *C. hamadryadella* suggests that *P. carolinensis* displays an aggregative response to *C. hamadryadella*. However, the lack of a statistically significant relationship between chickadee abundance and leaf-miner density in one year of our study suggests that the aggregative response is either not

particularly strong or at least it is difficult to detect given the small number of sites studied. Although our high density population of *C. hamadryadella* occurs in a planted oak grove and our low density populations occur in natural forest, we argue that differences in site characteristics other than the abundance of *C. hamadryadella* are not responsible for the observed differences in the abundance of *P. carolinensis* between sites. While we have no quantitative estimates of the abundance of *P. carolinensis* other than in 1994-1995, during 15 years of study at these sites *P. carolinensis* was only abundant at the oak grove site during outbreaks of *C. hamadryadella* (E. Connor, personal observation). Furthermore, an examination of guild specific insect damage to the leaves of *Q. alba* in the oak grove and one of the woodland sites indicates that only damage caused by leaf-mining insects, mostly *C. hamadryadella*, differs significantly between sites (Nuckols and Connor 1995).

Nevertheless, an aggregative response by *P. carolinensis* to *C. hamadryadella* was only observed at the scale of woodlands. Examination of the foraging time allocation of individuals and groups of chickadees in the oak grove indicates that *P. carolinensis* does not concentrate its search in trees with high densities of *C. hamadryadella*. Furthermore, *P. carolinensis* does not preferentially attack leaves with high densities of leaf mines. This result is consistent with observations reported by Brown *et al.* (1997) that *P. carolinensis* does not concentrate its foraging in the lower crown of *Q. alba* trees where the densities of *C. hamadryadella* are highest.

The functional response of *P. carolinensis* to *C. hamadryadella* is complicated. When *C. hamadryadella* enters an "outbreak," predation by *P. carolinensis* increases probably because individual chickadees develop search images for the formerly uncommon leaf mines. However, as *C. hamadryadella* density continues to increase, the per capita consumption rate of leaf mines by chickadees may actually decline for two distinct reasons: predator confusion and mechanical limitations to foraging.

First, chickadees may become confused and unable to localize prey when foraging on leaves with high densities of leaf mines. Chickadees are visually searching predators that probably use the contrast in color between mined and un-mined portions of leaves, and movement by larvae within leaves as cues to determine which leaves to attack and the location within leaves to attack. In the field, we have observed *P. carolinensis* to perch on an adjacent twig and visually inspect a mined leaf before attacking larvae on that leaf. Our data based on the use of human surrogates suggests that visually searching predators will be less efficient when searching leaves with a high proportion of the leaf area mined. This is because on leaves with a low proportion of the area mined, leaf mines appear as distinct blotches with a single larvae that is easy to visually locate within the boundaries of the mine. At maturity, mines of *C. hamadryadella* are approximately 2.5 cm² in area. On leaves with a high proportion of the area mined, mines coalesce and larvae are more difficult to locate since their movements are no longer restricted by the boundaries of individual leaf mines. Leaves of *Q. alba* average 50 cm² in area (Connor *et al.* 1997), and leaves with as few as 10 mines of *C. hamadryadella* may have substantial proportions of their area mined with many mines coalescing. On leaves with multiple mines that have coalesced, larvae are no longer easy to locate within a small area since they can occur anywhere within the much larger mined region.

Second, to attack *C. hamadryadella*, *P. carolinensis* uses a foraging behavior that may place mechanical limitations on their ability to attack multiple larvae within an individual leaf during a single foraging bout. After inspecting a leaf from an adjacent twig, *P. carolinensis* takes to the wing and grasps the leaf by the apex resulting in a posture in which the chickadee is hanging "upside down" from the leaf. Individual birds then lift or rock their bodies to peck at larvae within leaf mines on the leaf. This hanging "upside down" foraging behavior produces a rigid leaf, because the leaf supports the weight of the chickadee, against which the bird's beak can perform the work of

extracting the leaf-miner larva. Pecking at a leaf that is not immobilized by the weight of the bird would result in the leaf moving and hamper or prevent extraction of the leaf-miner larvae. However, the time spent hanging from a leaf may be limited by muscle fatigue associated with grasping the leaf, supporting the entire weight of the bird, and by movements required to attack leaf-miner larvae. While an individual bird could engage in multiple bouts of foraging on a single leaf, we suggest that this is unlikely since leaves with leaf mines are common in high-density populations.

Many authors have remarked on the tendency for a variety of species of birds in the family Paridae to use this hanging "upside down" foraging behavior when gleaning insects from the foliage of broad-leafed trees (Gibb 1954, Sturman 1968, Partridge 1976a,b, Robinson and Holmes 1982, 1984, Smith 1991). Species in the Paridae apparently use this hanging behavior more than any other group of foliage gleaning birds (Robinson and Holmes 1982). Morphological characters of the legs and modifications to the leg musculature appear to permit more common use of this hanging behavior by parids than other groups of birds (Partridge 1976a,b, Norberg 1979, Moreno 1990). Nevertheless, the duration of bouts of hanging and hence the ability of parids to consume large numbers of prey within a single leaf may be limited by muscle fatigue. Partridge (1976b) reported that the average duration of bouts of hanging by *Parus caeruleus* to be 6.5 seconds and for *Parus ater* to be 4.0 seconds when hanging from oak leaves. While we have no measurements of the duration of hanging bouts by *P. carolinensis*, if they are similar to *Parus caeruleus* then most larvae of *C. hamadryadella* on high density leaves could not be attacked within a single hanging bout.

Given the localized nature of the outbreak population we studied, a numerical response of *P. carolinensis* to *C. hamadryadella* density is unlikely. Combined with the lack of a strong aggregative response and the observed reduced foraging efficiency at high leaf-miner densities due to increased search time and mechanical limitations, the impact of predation by *P. carolinensis* on *C.*

hamadryadella is inversely density-dependent at all spatial scales. This pattern is consistent with the results of other studies on the impact of avian predators on high density or outbreak populations of forest insects, although in other instances outbreaks sometimes persist for sufficient time to produce numerical responses by avian predators (McFarlane 1976, Holmes 1990).

Hedges and Lawton (1983a) also found that predation by *Parus caeruleus* on *Phytomyza ilicis* was inversely density-dependent at all spatial scales. However, our results contrast with those of Itämies and Ojanen (1977a) who reported density-dependent predation by *Parus major* and *Parus montanus* on two species of leaf miners at the scale of woodlands. However, the combined densities of the two leaf-miner species in Itämies and Ojanen's (1977a) study ranged between 0.08 and 1.76 mines/leaf, and their study was conducted in the autumn when alternative insect prey are scarce. Our study examined *C. hamadryadella* populations whose density ranged as high as 40 mines/leaf, and during a time of the year when *P. carolinensis* was observed to readily take alternative prey. In combination, these two studies suggest that the tendency for parids to aggregate their attack on leaf-miner prey may depend in part on the density of the target prey species and on the availability of alternative prey species.

On first examination, the spatially inversely density-dependent impact of *P. carolinensis* on *C. hamadryadella* suggests that *P. carolinensis* contributes little to suppression of outbreak populations of *C. hamadryadella*, and may actually further destabilize the population dynamics of *C. hamadryadella*. However, our results do not necessarily imply that *P. carolinensis* is more effective in limiting the abundance of *C. hamadryadella* when *C. hamadryadella* is at low densities, as has been claimed for other systems of forest insects and avian predators (Holmes 1990). In 15 years of study, we only observed *P. carolinensis* to be a predator of *C. hamadryadella* during outbreaks. Therefore, even though the impact of *P. carolinensis* is spatially inversely density-dependent, *P.*

carolinensis is likely to exert a temporally density-dependent impact on *C. hamadryadella*.

Furthermore, the impact of *P. carolinensis* occurs in the context of other mortality factors such as the effects of other natural enemies and mortality caused by intra-specific competition, each of which has its own spatial and temporal density relationships.

The mortality pattern imposed by *P. carolinensis* in high-density populations of *C. hamadryadella* appears to complement that produced by intra-specific competition. In outbreak populations of *C. hamadryadella*, mortality caused by starvation due to intra-specific competition for the limited food resources within leaves is very strongly density-dependent at the leaf scale. Because the average leaf is 50 cm² in area, has 40 individual larvae, and each larva requires 2.5 cm² of leaf tissue to reach maturity, mortality due to intra-specific competition is inevitable for most larvae on high-density leaves even without positive density-dependent attack by *P. carolinensis*. Therefore, avian predation can only increase total generation mortality if it results in higher mortality rates for larvae on low-density leaves. Thus, the inversely density-dependent impact of *P. carolinensis* on *C. hamadryadella* at the leaf scale combines with the strongly positively density-dependent impact of intraspecific competition to result in greater population suppression than would have been realized given a positively density-dependent predator. However, the inversely density-dependent effect of *P. carolinensis* on *C. hamadryadella* at the leaf scale is similar to that exhibited by insect parasitoids (Connor and Beck 1993, Connor and Cargain 1994). Therefore, the suppression of high density populations of *C. hamadryadella* by *P. carolinensis* may be reduced because mortality caused by both sources displays the same density relationship and therefore is competitive, not complementary.

The literature on avian predation on leaf-mining insects, including behavioral studies, studies of predator impact, and studies of avian gut contents, only reports members of the family Paridae to be predators of leaf miners (Betts 1955, Szöcs 1959, Owen 1975, Itämies and Ojanen 1975, 1977a,b,

Heads and Lawton 1983a,b, Heinrich and Collins 1983, Connor and Beck 1993, Auerbach *et al.* 1995, Brown *et al.* 1997). This may reflect a lack of study or the tendency for studies of predation on leaf-mining insects not to identify the specific predators. Alternatively, we suggest that the modified leg musculature of the Paridae pre-adapts them for foraging on leaf-mining insects, particularly on broad leaf-plants, and this accounts for the widespread observation of parids as predators of leaf-mining insects.

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Table 1. Correlations between leaf characteristics and A) the time to discover the first mine, and B) the number of mines discovered in one minute.

A. Time to Discover First Mine	<i>r</i>	p	<i>n</i>
Average percent transmittance of light (400 - 700 nm)	0.149	0.431	30
Percent transmittance of light through first discovered mine	0.224	0.235	30
number mines/leaf	-0.081	0.670	30
number mines/cm ² leaf area	0.035	0.857	30
proportion of leaf area mined	0.409	0.025	30
<hr/>			
B. Number of Mines Discovered In One Minute	<i>r</i>	p	<i>n</i>
Average percent transmittance of light (400 - 700 nm)	0.262	0.161	30
Percent transmittance of light through first discovered mine	0.157	0.407	30
number mines/leaf	-0.161	0.396	30
number mines/cm ² leaf area	-0.184	0.330	30
proportion of leaf area mined	-0.377	0.040	30

FIGURE CAPTIONS

Figure 1. The density of foraging chickadees in relation to the density of *Cameraria hamadryadella* in the four study sites in A. 1994 ($r = 0.96$, $p = 0.041$, $df = 2$, chickadee density = $0.11(\text{number of mines/leaf}) + 0.15$) and B. 1995 ($r = 0.56$, $p = 0.44$, $df = 2$, chickadee density = $0.057(\text{number of mines/leaf}) + 0.15$).

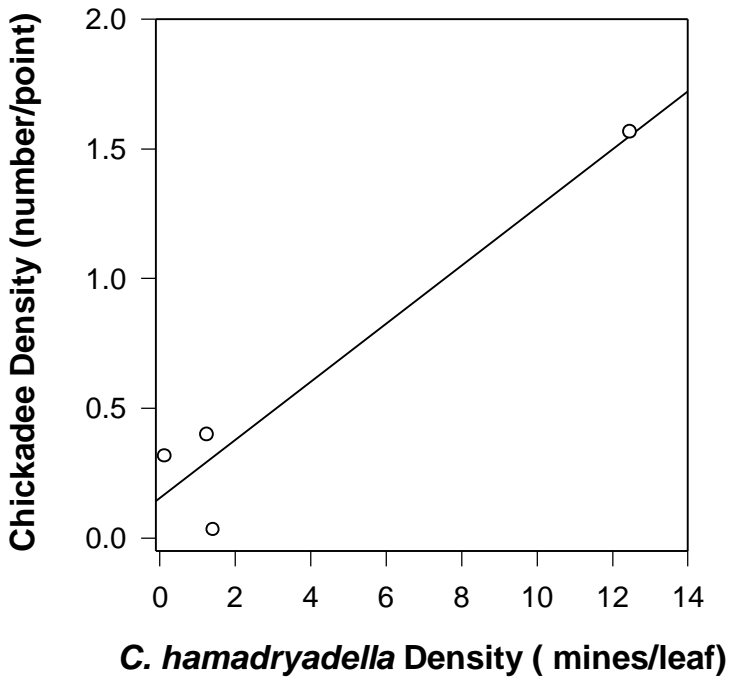
Figure 2. Foraging time investment of chickadees in relation to the density of *Cameraria hamadryadella* in individual trees at the oak grove site ($r = 0.10$, $p = 0.38$, $df = 71$, foraging time = $0.025(\text{number of mines/leaf}) + 3.2$).

Figure 3. The time to discovery of the first larvae (A) and the number of larvae discovered (B) by human subjects, serving as surrogates for chickadees, in relation to the proportion of the leaf area mined (A. $r = 0.41$, $p = 0.025$, $df = 28$, time to discover first mine = $14.3(\text{proportion of leaf area mined}) + 3.24$; B. $r = -0.38$, $p = 0.04$, $df = 28$, number of mines discovered = $-1.64(\text{proportion of leaf area mined}) + 2.99$).

Figure 4. Relationship between the proportion of mines preyed upon and the density of *Cameraria hamadryadella* for: A. woodlands ($r = -0.98$, $p = 0.018$, $df = 2$, proportion of mines preyed upon = $-15.75(\text{number of mines/leaf}) + 30.45$), B. trees ($R^2 = 0.15059$, $df = 18$, proportion of mines preyed upon = $0.144(\text{number of mines/leaf})^{-0.217}$), and C. individual leaves (random sample: $R^2 = 0.097$, proportion of mines preyed upon = $0.224(\text{number of mines/leaf})^{-2.21}$, $df = 541$); D. leaves observed to be foraged upon by chickadees ($r = -0.49$, $p = 0.034$, $df = 17$, proportion of mines preyed upon = $-0.02(\text{number of mines/leaf}) + 0.59$).

Figure 1

A. 1994



B. 1995

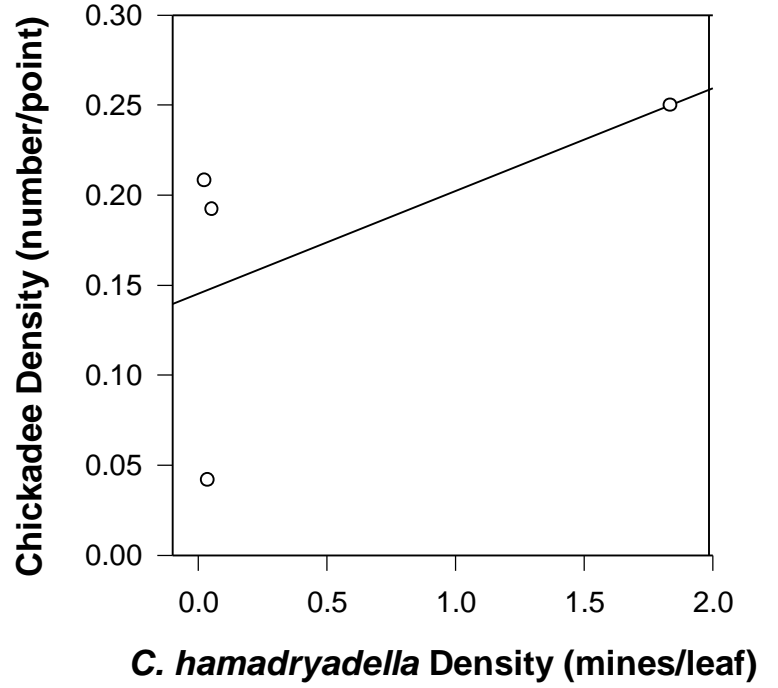


Figure 2

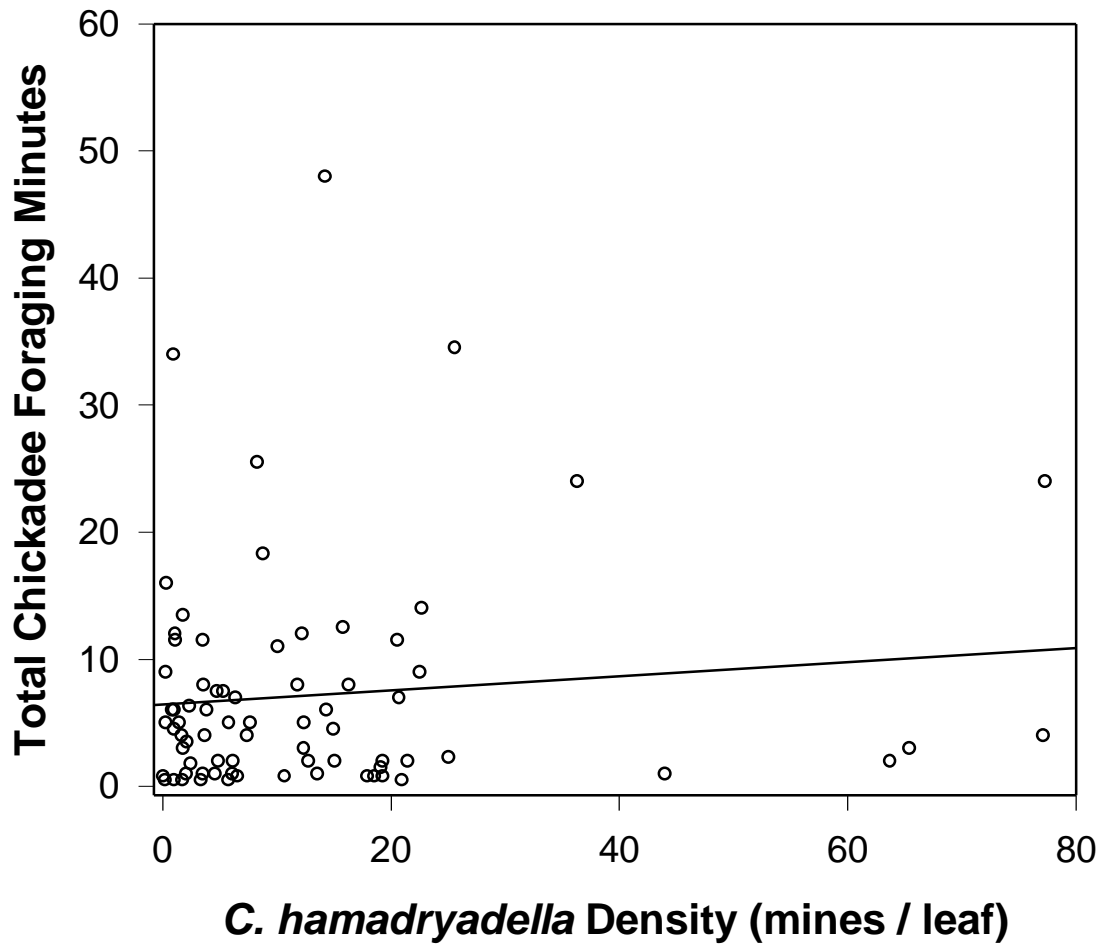


Figure 3

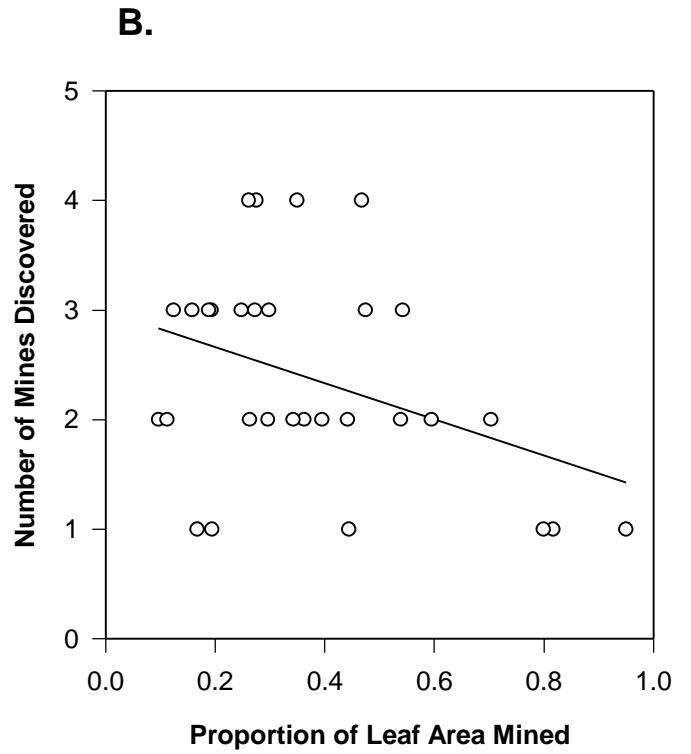
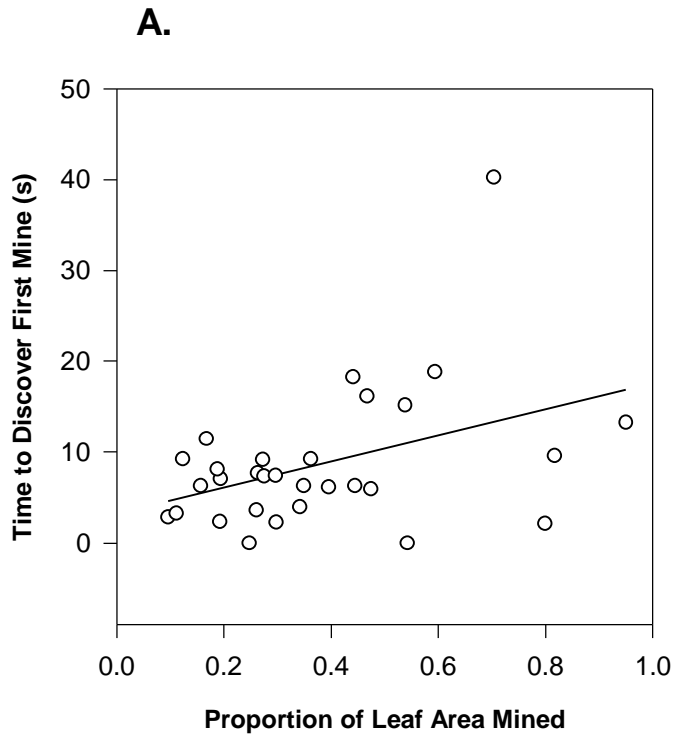
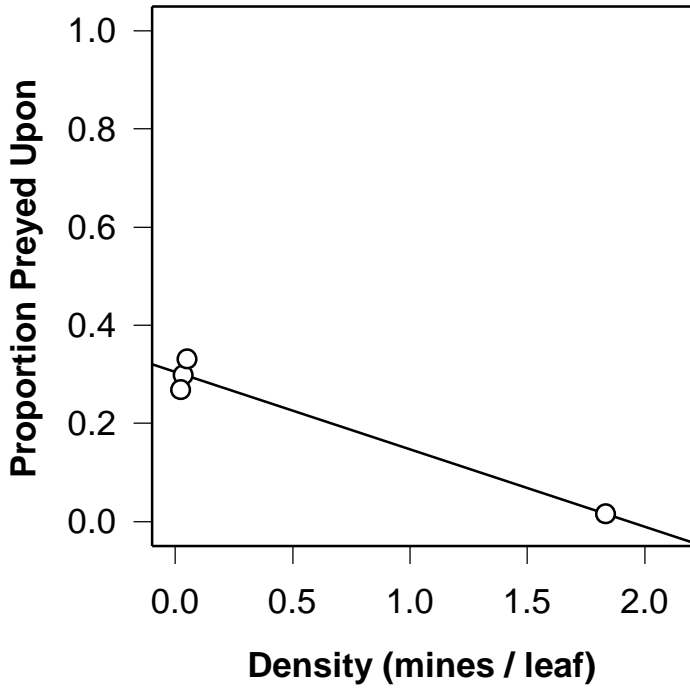
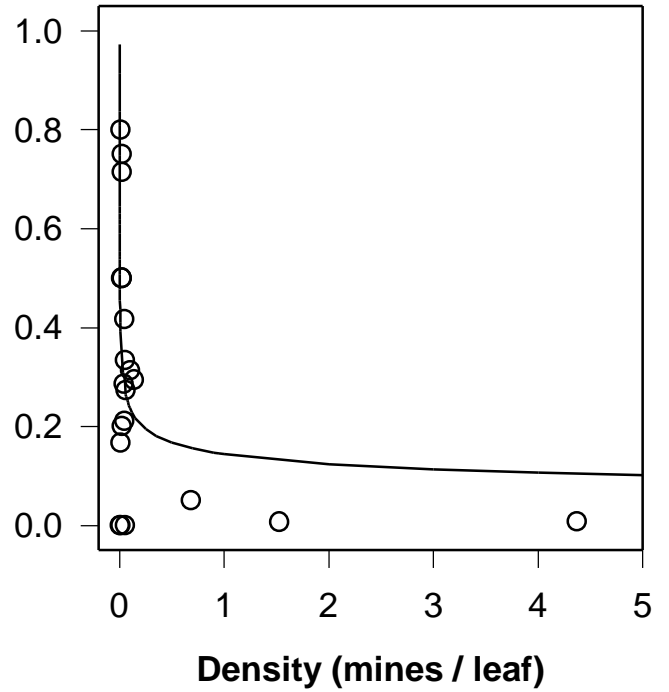


Figure 4

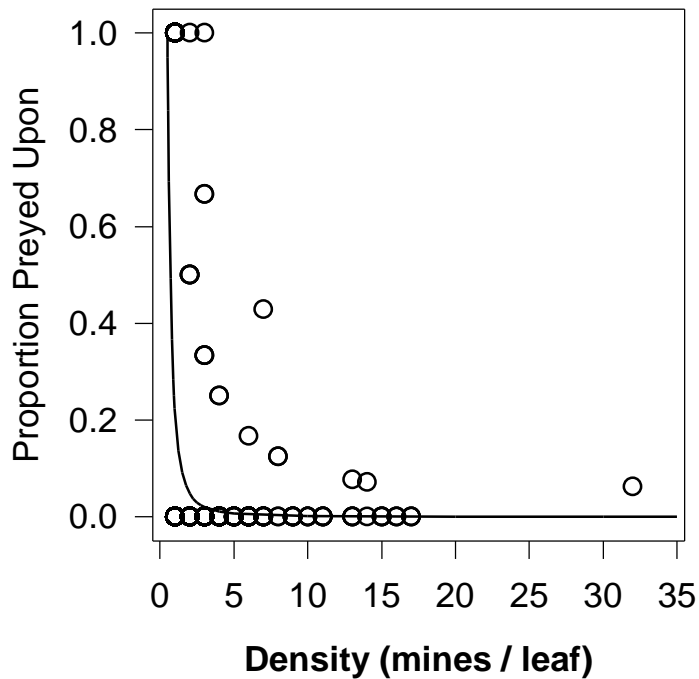
A. Woodlands



B. Trees



**C. Leaves
(Random Sample)**



**D. Leaves
(Selected by Chickadees)**

