

Quantification of Resources

ECOLOGICAL AND EVOLUTIONARY IMPACTS OF BIRD PREDATION ON FOREST INSECTS: AN OVERVIEW

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Abstract. Here I consider the effects of bird predation in both ecological and evolutionary time on forest insects: their abundances, morphological and behavioral characteristics, life histories, and other traits. Most information concerns the numerical impact of bird predation on defoliating Lepidoptera, especially those exhibiting population irruptions. Data indicate that birds have little effect on prey when prey are at outbreak densities. Although economically important and conspicuous, such irruptions are exhibited by relatively few Lepidopteran species, and even then they are often temporally and geographically patchy. I argue that these are unusual events and that the major foods of forest birds are insects that are most frequently at low or endemic population levels. Data, particularly those from the more quantitative and experimental studies, suggest that birds along with other natural enemies help maintain low abundances of such prey populations. This effect varies seasonally, being greatest during the birds' breeding periods when food demand is highest, and may result in frequent food limitation for insectivorous birds in temperate forests.

Another consequence of the apparently sustained and often strong numerical impact of bird predation is evolutionary. Birds, through their selective foraging, are thought to be an important evolutionary force in determining many traits of their prey populations. One such consequence for Lepidoptera larvae is to influence their life styles and feeding schedules which, in turn, determine the extent and patterns of their herbivory. In this way, birds through selective foraging indirectly affect other ecosystem components and processes. Such traits as crypsis, aposematism, restricted choice of feeding substrates, rigid feeding schedules, tissue or plant species preferences, and other features of insect life cycle organization appear often to be a result of selective pressures exerted by bird predation. Many of these traits are also influenced by interactions of the insects with their host plants, thus forming a diffuse coevolutionary system. The implications of this view are that birds are not simply frills in ecological systems, but exert through their foraging activities important influences in communities on both ecological and evolutionary time scales.

Key Words: Bird foraging; predation; selective foraging; evolutionary impact; insectivorous birds; defoliating Lepidoptera; forest insects.

The role of birds in natural ecosystems has long been discussed. A major issue has been whether or not birds exert any controlling influence on the numbers of their prey. Although this possibility has been considered for centuries (see Murton 1971), the first major scientific effort to evaluate such a role began with the studies of the U.S. Biological Survey in the early part of this century (e.g., McAtee 1932, Martin et al. 1951) and has continued largely through the efforts of forest entomologists (e.g., Morris et al. 1958, Campbell 1973). In general, results indicate that although birds consume large numbers of insects, they rarely seem to exert any controlling or regulating effect, at least not on high populations of economically important insects (see reviews by McFarlane 1976, Otvos 1979).

The possible roles of birds in ecosystem structure and functioning, particularly in energy flow and biogeochemical cycling, were considered during the International Biological Program era in the 1960s and early 1970s. These investiga-

tions showed that a small proportion of total energy and materials flowed through bird components of natural ecosystems, and largely concluded that birds had little direct effect on or involvement in ecosystem processes (Wiens 1973, Sturges et al. 1974, Holmes and Sturges 1975, Wiens and Dyer 1975). This led Wiens (1973: 265) to raise the possibility that birds in grasslands "... really are 'frills' in the ecosystem, living and reproducing off its excesses without really influencing it in any way." He predicted, however, that if birds have an important role, it would be as controllers of other ecosystem components (e.g., prey populations), through which considerably larger fluxes existed.

From more recent studies of the interactions between birds and their food resources, especially manipulative studies, it seems that birds, through their trophic relations, might have a more integral role in natural systems than has generally been attributed to them. This has been most apparent in studies of bird-plant interactions in

TABLE 1
QUANTITATIVE AND EXPERIMENTAL STUDIES OF THE NUMERICAL IMPACT OF BIRDS ON FOREST INSECTS, MOSTLY
LEPIDOPTERA

Organism	Life stage ^a	Population level	Method ^b	Reference
Eastern spruce budworm (<i>Choristoneura fumiferana</i>)	L	Lo, Hi	Density/consump.	Morris et al. (1958)
	L	M	Exclosure	Dowden et al. (1953)
	L	Lo, M, Hi	Density/consump.	Crawford et al. (1983), Crawford and Jennings (1989)
Western spruce budworm (<i>C. occidentalis</i>)	L-P	Lo, Hi	Exclosure	Torgersen and Campbell (1982)
Jack-pine budworm (<i>C. pinus</i>)	L	Lo	Density/consump.	Mattson et al. (1968)
Larch sawfly (<i>Pristiphora erichsonii</i>)	L	Lo, Hi	Density/consump.	Buckner and Turnock (1965)
	Ad	Lo, Hi	Density/consump.	Buckner and Turnock (1965)
Gypsy moth (<i>Lymantria dispar</i>)	L	Hi	Density/consump.	Inozemtsev et al. (1980)
Codling Moth (<i>Cydia pomonella</i>)	L-P	Lo	Exclosure	Solomon et al. (1976)
All leaf-dwelling lepidopteran larvae	L	Lo	Exclosure	Holmes et al. (1979c, unpubl. data)
Peppered moth (<i>Biston betularia</i>)	Ad	Lo	Experimental release/observ.	Kettlewell (1955)

^a L = larvae, P = pupae, Ad = adult stage.

^b See text for description of methods.

which birds have been shown to be important pollinators (e.g., Regal 1982) and seed predators or dispersers (e.g., Temple 1977, Thompson and Willson 1979, Herrera 1984a), influencing the evolution of various traits in their "prey" populations through selective foraging. Analogous effects of predators on their prey have recently been explored for terrestrial systems in general by Price et al. (1980) and for aquatic systems by Kerfoot and Sih (1987) and Sih (1987).

In this paper, I review the ecological and evolutionary impacts of insectivorous birds on their prey, with emphasis on their interactions with caterpillars (Lepidopteran larvae), which are an important food source, especially for birds in temperate forests (Royama 1970, Robinson and Holmes 1982). I recognize two major interrelated ways in which foraging insectivores influence prey species: (1) a numerical effect in ecological time by reducing prey abundances, and (2) an evolutionary effect by acting as selective agents that influence the prey's morphology, behavior, and life history characteristics, which in turn determine the activities and ecosystem roles of these insects.

THE NUMERICAL IMPACT OF BIRDS ON INSECT PREY

Quantitative assessments of the numerical impact of bird foraging have usually involved es-

timating bird densities and insect consumption rates, and then comparing the latter to estimates of the standing crops of insects in the field. This indirect method involves many assumptions and sources of error that may be compounded at each step in the calculations. Yet, for situations involving large numbers of birds and high densities of insects, it probably provides reasonable, albeit order-of-magnitude, estimates (e.g., see Dowden et al. 1953; Morris et al. 1958; Buckner 1966, 1967; Gage et al. 1970, Crawford and Jennings 1989). Experimental approaches provide more precise information on the impact of avian predators, but also have their problems: they are difficult to conduct in natural situations and often require great effort and expense to obtain information from both control and experimental plots with sufficient replicates to provide statistically meaningful results. Early attempts to remove birds from large forest tracts (e.g., Stewart and Aldrich 1951, Hensley and Cope 1951) or to exclude birds from small trees or single branches (Mitchell 1952) suffered from these difficulties. Several recent investigations, however, have used more rigorous and extensive experimental techniques.

The best data currently available on the effects of bird predation on forest insects, mostly Lepidoptera, come from a relatively few studies that have used either the bird density-prey consump-

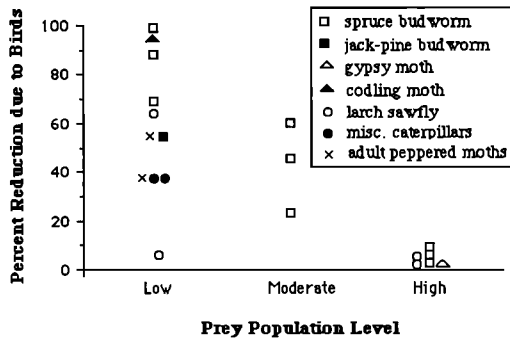


FIGURE 1. The impact of predation by forest birds on Lepidoptera as a function of prey density (see Table 1 for references and text for further explanation).

tion technique in a detailed and rigorous way, reasonably well controlled exclusion experiments, or studies of predation rates on released adult moths (Table 1). Because most such studies were done on prey populations that regularly undergo periodic irruptions (and often cause economic damage), I have classified the data from each study as being obtained during periods of low, moderate, or high population levels of the prey, based largely on the authors' assessments. High levels generally represent periods of insect outbreaks in which defoliation is extensive, moderate levels are those in transition before or after peak irruptions, and low levels reflect "normal," nonoutbreak conditions.

Comparison of results of studies listed in Table 1 reveals (Fig. 1) two major points. First, it seems that birds take only a small percentage of the available insects when they are present in high densities. Although they exhibit both numerical and functional responses to increasing prey densities (Morris et al. 1958, Sloan and Coppel 1968, Mattson et al. 1968, Gage et al. 1970, Holmes and Sturges 1975, Crawford and Jennings 1989), birds seem unable to respond sufficiently to influence the continued rise in the abundance of these prey (McFarlane 1976, Otvos 1979). Although birds cannot keep up with a rapidly expanding defoliator population, their relatively strong impact at endemic levels (Fig. 1) suggests that such predation could delay the onset of an outbreak, as suggested previously (e.g., Morris et al. 1958, McFarlane 1976, Otvos 1979). Indeed, modeling of spruce budworm populations suggests that predation by birds may be a significant factor in maintaining endemic population levels of this species (Peterman et al. 1979, see also Crawford and Jennings 1989).

The second point from Figure 1 is that the impact of bird predation is proportionately much greater when insects are at low densities. This is

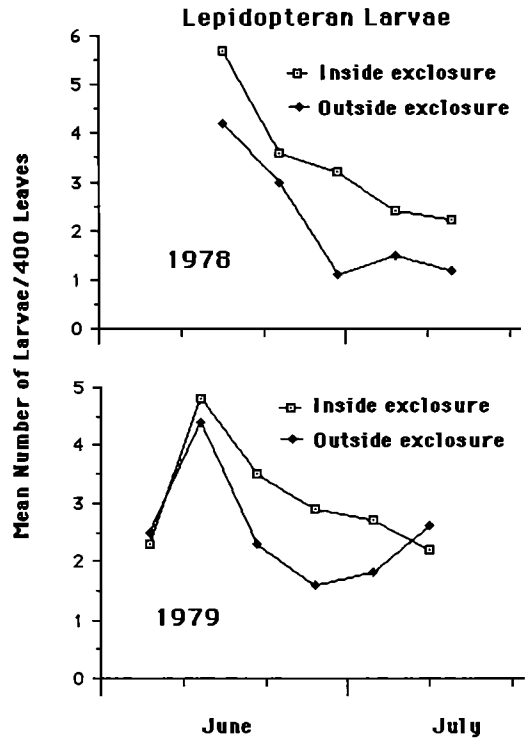


FIGURE 2. Densities of Lepidopteran larvae on foliage inside and outside of 10 exclosures in 1978 and 1979 in the Hubbard Brook Experimental Forest, N.H. Data from Holmes et al. (1979c) and Holmes and Schultz (unpublished).

further illustrated by experiments conducted by me and colleagues at the Hubbard Brook Experimental Forest in New Hampshire (e.g., Holmes et al. 1979c). In 1978 and 1979, we excluded birds from patches of understory vegetation and measured densities of all leaf-dwelling insects inside and outside of these exclosures. We moved exclosures to different patches of vegetation in 1979. In both years, the numbers of Coleoptera, Hemiptera, and spiders were not significantly different inside and outside of the exclosures, probably because these more mobile arthropods could readily move through the approximately 2-cm mesh netting. For Lepidopteran larvae, which are more sedentary, the numbers outside the exclosures were significantly reduced in several of the sampling periods (Fig. 2). Because other predators of these larvae, such as wasps or possibly ants, were not excluded by the netting, the reduction can be attributed almost entirely to birds. In the two years, birds reduced larval numbers by 20 to 63%, varying with the sampling period during the season; the average reduction in each season was 37%. The

periods of greatest impact of bird predation were in late June and early July in both seasons (Fig. 2), which were times when birds were feeding nestlings and fledglings and thus when food demand was probably greatest.

These results, along with those in the literature (see Table 1), suggest that birds can have significant numerical effects on insect populations at endemic levels. This finding is particularly significant in view of the fact that most forest-dwelling Lepidoptera and similar species in temperate forests typically occur at low densities and rarely if ever exhibit population irruptions (Morris 1964, Mason 1987b). Even the few species that irrupt become abundant for only short periods and then decline to low population levels for several years (Berryman 1987, Wallner 1987). Moreover, when outbreaks occur, they are often geographically patchy (Campbell 1973, Martinat 1984). The result is that any one forest stand may only occasionally experience an outbreak. For northern hardwood forests, this may be once every 10–20 years (Holmes 1988), much longer than the lifetime of most individual birds. Consequently, birds probably lack highly evolved systems for detecting and responding to such temporal and geographic variability, although a few species may do so (e.g., MacArthur 1958, Morse 1978b). Hence, while outbreaks provide a locally abundant food in some years and places, the endemic population levels of most Lepidoptera and other arthropods provide the majority of the food source for birds most of the time.

Available data, such as those in Table 1 and Figure 1, suggest that the low abundances of insect species may be maintained at least in part by heavy predation pressure from birds, although wasps (Steward et al. 1988b), ants (Campbell et al. 1983), small mammals (Smith 1985), as well as viral and other disease organisms, are undoubtedly involved in various combinations. This general importance of natural enemies in the regulation of herbivorous insects, while controversial (Hassell 1978, Dempster 1983), is also supported by studies of the prey organisms employing key factor analysis and other demographic techniques (e.g., Varley et al. 1973, Polard 1979, Mason and Torgersen 1987; also see Strong et al. 1984).

It is difficult to generalize about the numerical impact of birds on groups other than Lepidoptera, largely because of the lack of detailed or experimental studies. However, Gradwohl and Greenberg (1982b) showed through an exclusion experiment that tropical antwrens (*Mymotherula fulviventris*) reduced arthropods in dead leaf clusters by about 44%. Likewise, Askenmo et al. (1977) and Gunnarsson (1983) showed that birds removed 17–50% of spiders on spruce foliage

over the course of the winter. Other examples of birds reducing local abundances of insects are given by Stewart (1975), Bendell et al. (1981), Loyn et al. (1983), and Takekawa and Garton (1984), and many anecdotal records are cited by Murton (1971), McFarlane (1976), and others. Finally, numerous studies, some manipulative, have found significant effects of bird predation on the abundances of bark beetles and other bark-burrowing insects (see review by Otvos 1979). Taken together, these findings suggest that birds probably have significant numerical effects in a wide variety of habitats and ecosystems.

Finally, contrary to generalizations by Fretwell (1972) and Wiens (1977) that limitation of many temperate bird populations may occur primarily in the winter, evidence is accumulating that food may often limit insectivorous bird populations in the temperate summer (Martin 1987). Recent studies at Hubbard Brook in New Hampshire, for example, indicate that food becomes abundant only during insect outbreaks, which occur sporadically and infrequently (Holmes et al. 1986, Holmes 1988). Birds in these deciduous forests depend heavily on non-irrupting prey, whose abundances they further depress during the breeding period (Holmes et al. 1979c; see above) at a time when the growth and survivorship of newly hatched young are greatly affected (Rodenhouse 1986). Birds in this temperate deciduous forest appear to experience prolonged periods of food limitation (Rodenhouse and Holmes, in prep.) partly because of the strong numerical effect exerted by the birds themselves.

I conclude that birds in temperate forests may exert a strong numerical impact on their arthropod prey, and that this may occur most often during the height of the breeding period. The effect may be to depress or maintain insect numbers at low levels and, in the case of prey species that exhibit population irruptions, to extend the periods between such events. This is consistent with the syntopic population model developed by Southwood and Comins (1976) in which an "endemic ridge" is separated from an "epidemic ridge" by a "natural enemy ravine." More large-scale experiments on the impact of birds and other enemies on endemic prey populations will clarify the extent and influence of such interactions. Extending such studies of the impact of bird predation on defoliators to tropical or other ecosystems, or to other kinds of arthropod prey, should be an important priority.

THE EVOLUTIONARY IMPACT OF BIRDS ON THEIR INSECT PREY

In the long term, the important effect on insect prey of intensive foraging by birds will be evolutionary. For example, the 37–57% predation

rates recorded by Kettlewell (1955, 1956, 1973; see Table 1) on the peppered moth have been generally accepted as evidence of strong selection by birds for the evolution of morphological and behavioral traits in this insect (Cook et al. 1986, Endler 1986; but see Lees and Creed 1975). Since available evidence indicates that predation at this level by birds may be common (e.g., Table 1, Fig. 1), it seems likely that birds could have had, and continue to exert, a strong selective influence on their prey. The possibility that birds and other predators have an evolutionary impact on patterns of crypsis and other supposed predator-avoidance traits in insects has long been recognized (e.g., McAtee 1932, Cott 1940) and seems to be more or less taken for granted by many biologists (but see Endler 1986). However, ramifications of bird predation go beyond the evolution of crypsis or other antipredator traits that have not, in my opinion, been adequately considered. These include influences on the life-styles, feeding patterns, and other characteristics of these insects, which in turn affect their involvement and role in ecosystem processes, as I discuss below.

BIRDS AS SELECTIVE AGENTS ON INSECT MORPHOLOGY AND BEHAVIOR

Birds have long been implicated as a major agent of selection for aposematism (Harvey and Paxton 1981) and mimicry (Wickler 1968, Robinson 1969), as well as for nonmimetic polymorphisms in various prey populations (e.g., Cain and Shepherd 1954, Allen 1974, Wiklund 1975, Mariath 1982). Differential predation by birds affects the sex ratio of their prey (Bowers et al. 1985, Glen et al. 1981). Baker (1970) proposed a variety of ways in which predation by birds may have influenced evolution of the sizes, shapes, colors, and behavior of larval and pupal stages of *Pieris* butterflies, and Sherry and McDade (1982) inferred importance of bird predation on the shapes and sizes of tropical insects. Also, the evolution of spines, hairiness, and other similar features of insects and other prey are usually considered to be anti-predator adaptations (Root 1966, Edmunds 1974). Waldbauer and associates (Waldbauer and Sheldon 1971, Waldbauer and LaBerge 1985) proposed that the early-season occurrence of certain hymenopteran-mimicking Diptera was due primarily to strong selection pressures by inexperienced birds foraging in midsummer. Relevant to all of these examples, however, Robinson (1969) pointed out the paucity of experimental evidence concerning the adaptiveness and selective forces influencing such presumed anti-predator traits. Two decades later, this still appears to be the situation.

Nevertheless, passerine birds have been shown to be able to distinguish between shape (Brower 1963), color (Jones 1932, Schmidt 1960, Brower et al. 1964, Bowers et al. 1985), and pattern (Blest 1956, Sargent 1968), which gives them the potential for being discriminate foragers (Curio 1976a). In some early experiments, Ruitter (1952) showed that birds could distinguish geometrid caterpillars from similar inanimate objects (twigs), although movement of the prey was often required for this process to occur. Further, Pietrewicz and Kamil (1977) showed that Blue Jays (*Cyanocitta cristata*) could discriminate cryptic *Catacola* moths on bark, and Mariath (1982) demonstrated that predation rates by birds varied with the proportion and spatial distribution of two morphs of a geometrid caterpillar and with the color of the plant background. Jeffords et al. (1979) painted diurnally flying moths to look like swallowtail and monarch butterflies, and showed that predators, mostly birds, distinguished among the different colors and patterns. Moreover, Chai (1986) showed that jacamars (*Galbula ruficauda*) discriminated among tropical butterflies on the basis of color and of taste, supporting the hypothesis that birds exert strong selection pressures influencing the evolution of mimicry patterns in butterflies. Not all evidence is positive, however. Lawrence (1985), for example, found that European Robins (*Erithacus rubecula*) and Great Tits (*Parus major*) did not easily learn to detect cryptic prey.

The degree to which an insect or other prey item is detectable probably depends most strongly on its choice of substrate and on its movement patterns. Those that choose an inappropriate substrate or that move at the wrong time should be more subject to predation. Wourms and Wasserman (1985) showed experimentally that prey movement influences birds' feeding choices, and Sherry (1984) described how the behavior of certain insects, including their movement patterns, makes them differentially susceptible to bird predators. Since most birds in terrestrial habitats are diurnally active predators that hunt by visual means, they will be actively searching for and taking prey from a variety of substrates, and any prey organism on the wrong background, moving actively, or being otherwise conspicuous will be quickly removed. With many different bird species occupying a single habitat, each with different searching techniques and methods of prey capture (Smith 1974b, Robinson and Holmes 1982, Gendron and Staddon 1983, Lawrence 1985, Holmes and Recher 1986a) and each being fairly opportunistic and catholic in its prey preference (MacArthur 1958, Rotenberry 1980a, Robinson and Holmes 1982, Sherry 1984), the

risk of predation is potentially high. Among the bird species in northern hardwoods forests, for example, some closely scrutinize nearby substrates as they move along branches and twigs, some examine undersurfaces of branches and leaves, while others move rapidly and flush prey from the foliage and twigs (Robinson and Holmes 1982). Furthermore, some forest birds differentially search and take prey from upper versus lower leaf surfaces (Greenberg and Gradwohl 1980, Holmes and Schultz 1988) and from particular plant species (e.g., Holmes and Robinson 1981, Holmes and Schultz 1988). They also may use leaf damage caused by chewing insects as prey-finding cues (Heinrich and Collins 1983) or develop search images (Tinbergen 1960) and other forms of learning (Orians 1981) to locate potential prey. All of these factors make it difficult for the prey to go undetected, and likely have led to the evolution of the observed anti-predator traits.

The main points are that birds discriminate foragers and that they use the appearance and behavior of their prey as major cues for locating those prey. These findings, coupled with the possibility that birds are often food-limited and that they can depress the numbers of their prey (except during insect outbreaks), implicates birds as important and significant selective forces that influence the evolution of many antipredator traits found among insects and other prey organisms.

ECOLOGICAL CONSEQUENCES OF THE EVOLUTION OF ANTIPREDATOR TRAITS BY INSECTS

As reviewed above, most considerations of the evolutionary effects of predators on prey have focused on the morphological (e.g., size, shape, color, hairiness) and behavioral (e.g., background choice, startle responses) traits of the prey. However, other equally interesting and important consequences or ramifications of such traits affect the life-styles and ecology of these prey organisms. For instance, consider a caterpillar that mimics a twig. It must remain motionless on its correct substrate for its crypsis to be effective, and any movement or change in substrate, at least during the day, is likely to increase the probability of its being detected by a foraging bird. Its feeding may therefore be restricted to night hours when its risk of predation by birds is lowest. These constraints in turn affect the ways in which the caterpillar feeds, and hence its pattern of herbivory. Herbivorous insects in temperate forests typically consume <10% of annual leaf production per year (Mattson and Addy 1975, Schowalter et al. 1986); this low level may result in part from the constraints imposed on the ma-

nor herbivores, namely caterpillars, by their antipredator adaptations (i.e., indirectly by bird predation) and partly by their interactions with the variable quality of the green leaves on which they feed (see below). The hypothesis that I want to develop here is that bird predation, acting in concert with the host plant and other factors, produces selective forces that act to organize and consequently influence the life history patterns—particularly feeding schedules—of leaf-chewing forest insects. The arguments are similar to those of Price et al. (1980), but focus specifically on bird-insect-plant interactions in forest habitats.

Because caterpillars do not mate, defend territories, or feed young (Schultz 1983a), their main “goals” are to accumulate biomass as rapidly as possible and to avoid being killed by natural enemies (i.e., parasites, disease, and invertebrate predators as well as foraging birds; Heinrich 1979c, Schultz 1983a). Means of achieving these goals may conflict. As argued by Schultz (1983a), maximizing feeding time and food quality should involve feeding throughout the day and night and because of variable food quality (see below), the larva may need to move frequently in search of new feeding places. At the same time, to avoid predation, the insect should minimize exposure during feeding, which, if diurnally hunting predators are important, might be done by feeding only at night or at least by restricting movement during daylight hours (Schultz 1983a).

The situation is complicated because the quality of leaves for herbivorous insects varies seasonally (Feeny 1970, Schultz et al. 1982), from tree to tree, from one leaf to another (Schultz 1983a, b), and even among different parts of a single leaf (Whitham and Slobodchikoff 1981). On sugar maple (*Acer saccharum*) and yellow birch (*Betula allegheniensis*) trees at Hubbard Brook, for instance, adjacent leaves on a single branch differ in chemical and physical properties important to herbivorous insects (Schultz 1983b). Since caterpillars are capable of discriminating among chemical cues (Dethier 1970) and of making behavioral “choices” of places to feed (Schultz 1983a), they should be able to respond to such local variation, although this has not been well documented (see below). Furthermore, short-term changes in phenolics and other defensive compounds can be induced by physical damage to the leaves, such as that caused by tearing or chewing (Haukioja and Niemala 1977, Schultz and Baldwin 1982, Baldwin and Schultz 1983, West 1985, Bergelson et al. 1986, Hunter 1987). Silkstone (1987) found that larvae fed less on damaged leaves, while Bergelson et al. (1986) showed that simulated damage to single leaves resulted in a significant increase in phenolic com-

pounds within several days and that larvae moved away from these areas, grew more slowly, and took longer to reach the pupal stages.

Such short term induction of defensive chemicals, if widespread, implies that the longer a caterpillar stays on a leaf, the higher the probability that it will become less palatable. Thus, to optimize feeding and growth, caterpillars may need to move periodically to new leaves in search of higher-quality feeding sites. This results in a trade-off situation: if it feeds and moves extensively during the day, it would be subject to high predation; if it feeds only at night and remains motionless through the day, it would probably not only grow more slowly but also take longer to reach the pupal stage. The latter is important because longer development means the larvae will be exposed longer to natural enemies, including parasites and disease (Pollard 1979, Schultz 1983b, Dammon 1987). Also, in temperate zones, night temperatures in spring and early summer are often cool, which might increase the energetic costs of searching at night, as well as further slowing metabolic processes and therefore growth.

If this scenario is correct, one would expect some relationship between feeding behavior and the antipredator traits of the prey. Surprisingly, little quantitative or experimental data exist on the ecology and behavior of caterpillars with respect to food choice and predation risk, and most of what does exist is anecdotal. Heinrich (1979c) reported that the feeding strategies and time budgets of palatable caterpillars were consistent with their need to minimize predation. The species he observed either fed only at night or stayed on the underside of leaves, and often moved from feeding sites after eating only small amounts of leaf tissue. They also often clipped off partially eaten leaves after feeding on them, which he proposed was an antipredator trait reducing the chances that birds would find the larvae by using leaf-damage cues (Heinrich 1979c, Heinrich and Collins 1983). Unpalatable larvae did not cut off partially eaten leaves, and were often seen exposed while resting and feeding on leaf surfaces during daylight hours (Heinrich 1979c). Bergelson and Lawton (1988) found that larvae of two Lepidopteran species moved relatively little in response to foliage damage, but became more vulnerable to predation by ants, but not by birds, when experimentally forced to move.

Schultz (1983a) found that caterpillars are often specific in their choices. He also described observations of feeding caterpillars that appeared to taste (mandibulating leaf edges) and often reject feeding sites. Lance et al. (1987) report similar behavior by gypsy moth (*Lymantria dispar*)

larvae. These observations suggest that some of the partial chewing of leaves reported by Heinrich (1979c) may in fact have represented food choice and later rejection by the caterpillar rather than a predator avoidance trait. On predation risk, Dammon (1987) showed that pyralid caterpillars survived better in leaf rolls than when exposed openly on leaf surfaces, and those on the undersides of leaves survived better than those on upper surfaces. In addition, the risk factor was apparently so important that the larvae chose leaves that were low in food quality. Hairy caterpillars, which are generally less preferred by avian predators (Root 1966, Whelan et al. 1989) might be expected to survive better or to have different feeding patterns from smooth-skinned, cryptic larvae. However, I am unaware of any study that has made such a comparison.

Caterpillars of some species in the forest at Hubbard Brook differ in feeding schedules and patterns of crypsis, which appear to reflect different evolutionary responses to predation risk (Schultz 1983a). For example, *Pero honestaria* (Geometridae) remains motionless all day on large twigs and branches far from feeding places, where it closely matches the background; at night it moves long distances from its resting sites to feeding areas and feeds during the dark hours. A closely related geometrid species, *Anagoga ociduaria*, feeds during both the day and night, but possesses a cryptic pattern that matches the small twigs and petioles near the leaves where it feeds; it is then able to "lean" over and take bites out of leaves during the day with only minimal body movement (Schultz 1983a). Another geometrid, *Cepphis armataria*, matches its own feeding damage on the leaves and thus remains in feeding position throughout the day and night; it feeds around the clock. Thus, different patterns of crypsis seem to allow insects to exploit their food in different ways. This comparison of closely related species is all the more interesting because they co-occur on the same host plant, striped maple (*Acer pensylvanicum*).

Although many of these ideas need experimental verification, and more information is needed on the interactions between bird foraging and prey defenses and feeding, the implications from the hypotheses developed here are that the evolutionary impact of bird predation, although indirect, has important ramifications on the life styles of the prey organisms and affects the structure and functioning of other ecosystem components. Birds are therefore not simply frills in ecological systems, as suggested by Wiens (1973), but exert through their foraging activities important influences in communities on both ecological and evolutionary time scales.

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