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there were slightly more individuals out-

side than inside the netting. Although

birds in this forest do prey on these ar-

thropods (8), their effect was either negli-

gible or unmeasurable in this experiment

Table 1. Densities of the major arthropod taxa

on leaves of striped maple inside and outside of exclosures. Numbers per 400 leaves

(mean \pm 95 percent confidence limits) were

based on samples taken from ten exclosures

and ten controls at eight weekly intervals dur-

ing the period 15 June through 10 August

Controls

 $5.5 \pm .92$

 $2.2 \pm .48$

 $1.3 \pm .31$

 $1.9 \pm .46$

 $2.3 \pm .44$

Р

.84

08

.86

.95 .003

Exclo-

sures

 $5.3 \pm .88$

 $1.7 \pm .37$

 $1.4 \pm .53$

 $2.3 \pm .74$

 $3.3 \pm .53$

12 June 1979; revised 27 August 1979

Bird Predation on Forest Insects: An Exclosure Experiment

Abstract. Exclusion experiments show that birds significantly reduce densities of larval Lepidoptera on forest understory vegetation. When insect densities are already low, bird predation may act both as a population regulator and as a strong agent of natural selection.

1978.

Taxa

Arachnida

Coleoptera

Homoptera

Hemiptera

Lepidoptera larvae

Insectivorous birds can be expected to influence their prey populations in at least two major ways. First, they may act as regulators of insect abundance, an effect that has been the subject of lengthy debate, especially as it applies to herbivorous insects (1). Second, as visually hunting predators, they may exert strong selective pressures that result in the evolution of crypsis or other predator-avoidance adaptations among their insect prey (2). Few data, however, exist on the actual impact of birds on their prey in nature (3). We report experimental evidence that birds depress the abundance of free-living defoliating insects in a temperate deciduous forest.

In 1978, we measured the impact of bird predation in the summer on endemic levels of foliage-dwelling arthropods in a northern hardwood forest (4). We used crop protection netting (5) to exclude birds from patches of striped maple (Acer pensylvanicum L.), an understory shrub (6). Ten exclosures, measuring about 6 by 6 by 2 m high, were established in early June after leaf flush was complete. An area of approximately equal size, similar plant species composition, and foliage density was chosen near each exclosure to serve as a control. At weekly intervals from 15 June through 10 August, we selected 400 striped maple leaves within each exclosure and each control area, and visually made a census of all insects present on the leaves and adjacent petioles and stems (7).

The results differed among the arthropod groups. For Arachnida, Coleoptera, Homoptera, and Hemiptera, we observed no significant differences in densities between the control and the experimental groups in any single sampling period, or for the season as a whole (Table 1). Indeed, in some sampling periods,

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perimental Forest (12).

because of the relatively high mobility of these kinds of prev.

The numbers of the more sedentary Lepidoptera larvae (9), however, were always higher inside the exclosures than outside (Fig. 1A). Because variances in the density data approximated the means, large differences were needed for statistical significance (10). When the numbers of Lepidoptera larvae are considered for the season as a whole (Table 1). significantly fewer Lepidoptera (P < .003) were found outside than inside the exclosures. In addition, we could distinguish statistically significant differences in the abundances of Lepidoptera larvae on two sampling dates, 29 June (P < .02) and 21 July (P < .05).

Since birds are the only element in the system excluded by the netting (11), we estimate from Fig. 1A that the weekly removal rates of caterpillars from understory foliage by birds range from 18 to 63 percent, averaging 37 percent. This effect is most extreme in late June and mid-July (Fig. 1A), coinciding with the nestling and fledging periods of insectivorous birds in this forest (12). During this part of the summer the numbers and biomass of birds hunting or needing to be fed nearly doubles (Fig. 1B), and their predation intensity must increase accordingly. The birds primarily responsible for this predation in the understory at Hubbard Brook were two warblers (Seiurus aurocapillus and especially Dendroica caerulescens), two thrushes (Catharus ustulatus and C. fuscescens), and several species that expand their vertical foraging ranges into the understory during the nestling and early fledgling periods (Vireo olivaceus, V. philadelphicus, and Setophaga ruticilla). That Lepidoptera larvae are a major food for most passerine birds, especially when young are being fed (8, 13) explains why the more significant depression of caterpillar numbers occurs at this time.

The proportion of the caterpillar standing crop removed in our experiment greatly exceeds the 0.1 to 1 percent reportedly taken by birds during most caterpillar outbreaks (14, 15). This suggests that, although birds seem to be unimportant as control agents during insect epidemics, they can depress further the numbers of caterpillars when the latter are already at low densities. Our results therefore provide experimental evidence supporting the suppositions of Tinbergen (16), Morris et al. (15) and Campbell and Sloan (17) that bird predation may be most effective at endemic prey population levels. The effect at these times is to reduce insect numbers at least locally

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60 Lepidoptera larvae leaves Inside exclosures --• Outside exclosures 40 Numbers/4000 20 0 ⁴⁰⁰ JB ha Bird populations bers/10 200 Num n



in ten outside control plots (asterisks indicate

their fledged young in the Hubbard Brook Ex-

< .05). (B) Densities of adult birds and of

and during certain parts of their life cycles and, possibly, as suggested by Morris *et al.* (15), to extend the time between insect outbreaks.

The long-term and possibly more significant effect of such heavy predation on already low densities of Lepidoptera larvae must be evolutionary. By acting as a strong selective force, bird predation can influence many of the prey's morphological, behavioral, and life-history traits and, in turn, their role in ecosystem processes. For instance, the heavy midsummer bird predation that we document here may not only select for patterns of crypsis in Lepidoptera larvae, but also for their choice of substrates on which to hide, their feeding schedules, and even the timing of their life cycles. We suggest that any or all of these effects will influence when or where a particular species of caterpillar feeds and thus its pattern of leaf consumption. The evolutionary effects of predation therefore have ecological consequences for the prey and their host plants.

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- Toron crop protection netting (Cissel, Farmingdale, N.J.) was suspended from ropes stretched between trees and secured to the 5. ground. The mesh was small enough (2.2 cm) to prevent entrance by birds, but did not appear to affect movements of flying insects (see results) or ovipositing moths, as judged by the similarity of taxa and size classes of Lepidoptera larvae nside and outside the exclosures.
- This understory plant was chosen because it is host to relatively high and less variable insect densities than are saplings of the dominant tree species (J. C. Schultz, in preparation), it can be easily enclosed, and the insects on its large leaves are readily observed and counted.
- leaves are readily observed and counted. This visual inspection method permits continu-ous, nondestructive sampling and is more accu-rate than other methods (J. C. Schultz *et al.*, in preparation). Other insect censuses conducted simultaneously on the same plant species, as part of a larger research program on forest in-sects, yielded densities and faunal composition similar to those in this avaciment 7. similar to those in this experiment

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Experimental Phenylketonuria: Replacement of Carboxyl Terminal Tyrosine by Phenylalanine in Infant Rat Brain Tubulin

Abstract. In the brains of newborn rats, about half of the tubulin molecules are modified posttranslationally by the addition of an aromatic amino acid at the carboxyl terminus of the α chain. Of the added residues, 96 percent are tyrosine and 4 percent are phenylalanine. After induction of hyperphenylalaninemia, the proportion of tubulin molecules containing carboxyl terminal phenylalanine increases up to eightfold and the pool of tyrosine-containing molecules decreases by an equivalent amount.

Human phenylketonuria is a disease in which a brain dysfunction is associated with an inherited deficiency of phenylalanine 4-hydroxylase (E.C. 1.14.16.1) in the liver (1). The metabolic sequela of this deficiency is an excess of phenylalanine, which accumulates in the blood and spinal fluid and leads to elevated brain phenylalanine. Experimentally, hyperphenylalaninemia has been produced in animals (2, 3) to study the biochemical abnormalities associated with the disease. The studies in animals have indicated that the biochemical characteristics of phenylketonuria can be induced, provided the treatment is administered early during development (2, 3). However, efforts to explain the pathogenesis of the brain damage have had no success.

In an unrelated study in chick brain we showed that a unique modification of tubulin, the posttranslational addition of aromatic amino acid residues to the carboxyl terminal end of the α chain (4), was enhanced in early development (5). A tubulin-specific ligase catalyzed the reaction (6) and tyrosine and phenylalanine competed for the binding site on tubulin (7). Direct quantitative analysis of the carboxyl terminal aromatic residues of purified tubulin from normal chick brain showed that tyrosine was the main modifier residue; phenylalanine modified no more than 2 percent of the tubulin molecules in young animals (5). This was consistent with the kinetic data for the reaction in vitro and the concentration in brain of each amino acid. Although the biological significance of this ligase reaction, which seems to be specific for α tubulin, is not known, the presence or absence or even the identity of an aromatic residue at the carboxyl terminal end of the tubulin molecule could conceivably affect the interrelationship between microtubules and other elements of the cell. Since microtubules appear to be essential for neuronal growth and function, a possible link between the phenylalanination of tubulin and the phenylketonuric condition seemed to be worth exploring.

We now report experiments in which we determined the state of modification of cytoplasmic brain tubulin in normal and hyperphenylalaninemic immature rats. Carboxyl terminal tyrosine and only small amounts of carboxyl terminal phenylalanine were present in about half of the molecules of tubulin in normal rats. In tubulin from the experimental animals phenylalanine substituted for a large proportion of carboxyl terminal tyrosine, although the availability of free carboxyl terminal sites for incorporation of amino acid in vitro was not affected.

Elevation of brain phenylalanine content was induced in albino male rats (Holtzman) by one of two procedures:

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