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DISTRIBUTION OF CECROPIA MOTH (SATURNIIDAE) IN CENTRAL ILLINOIS: A STUDY IN URBAN ECOLOGY

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ABSTRACT. Searches for cocoons and trapping adult males with virgin females showed that, in central Illinois, *Hyalophora cecropia* is rare in forests and old urban residential areas, uncommon in willows and other trackside and roadside vegetation, but abundant in new urban residential areas. The new residential areas built on crop fields, and the tracksides and roadsides have small trees and shrubs and resemble an early stage in succession. The forests and old residential areas have large trees and shrubs, and resemble a late stage in succession. We suggest that the cecropia moth is a fugitive species that "flees" to early stages in the succession. The availability of food plants cannot be the cause since acceptable hosts occur in all of the areas. The difference in the population size between rural and urban areas is at least partly explained by a difference in small mammal populations. *Mus musculus,* the most commonly trapped small mammal in residential areas, will eat naked cecropia pupae in the laboratory, but will not open cocoons to obtain the pupae. *Peromyscus leucopus* and *P. maniculatus,* the most commonly trapped small mammals in rural areas, readily open cecropia cocoons in the laboratory. Low-spun cocoons with injury typical of *Peromyscus* are frequent in tracksides and roadsides, but are almost never found in town. Woodpeckers prey heavily on both urban and rural high-spun cocoons. The small cecropia population in old residential areas and woodlands may be explained by the presence of caterpillar-feeding birds that are absent or scarce in the other areas. Cocoons were placed for the winter in woodlands to determine if mice or woodpeckers would attack them despite the absence of a natural cocoon population. Almost none of the cocoons taped near ground level were attacked by mice or other predators. Cocoons taped high in saplings were seldom attacked by woodpeckers, but were heavily attacked by an unidentified predator, probably the fox squirrel, *Sciurus niger.*

In 1965 we began long term studies of the cecropia moth, *Hyalophora cecropia* (L.) (Saturniidae). Intensive searching for cocoons in Champaign Co., Illinois, showed them to be rare in rural areas, almost absent in woodlands, and scarce in roadside and trackside woody vegetation. They were abundant in new urban residential areas but scarce in old urban residential areas. We report the results of systematic searching for cecropia cocoons in the winter and of trapping adult males in the summer, and discuss the distribution of this species in relation to land use, vegetative cover, and predation pressure.

Champaign Co., in east central Illinois, is highly agricultural. Over 90% of its land is in field crops; the original prairie and forests have almost disappeared. The towns and cities, planted with ornamental trees and bushes, are thus islands of urban forest in a sea of cropland. Natural forests are limited to a few small upland tracts and narrow

strips along the larger rivers. A few small woody plants grow on railroad and highway rights-of-way and in fence rows.

Several reports indicate that cecropia is generally uncommon in rural and wild areas, but that it may have unusually high populations in some urban areas. Smith (1899 and 1908) found cecropia to be particularly abundant in cities in New Jersey and on Long Island, New York. Thompson & Fiske (1909) found large numbers of cocoons only by collecting in cities in New Hampshire, Massachusetts, New York and New Jersey. Porter (1912) found many cocoons in Indianapolis, Indiana but reported only a few from rural Indiana. Cocoons were reported to be abundant in Chicago, Illinois, by Downing (1921) and Marsh (1937) and in Champaign and Urbana, Illinois, by Sternburg & Waldbauer (1969) and Waldbauer & Sternburg (1973). Few workers report cecropia to be abundant in rural or wild areas. Maughan (1906) found many cocoons in a swampy grove in Ontario. In reporting a find of 79 cocoons in a grove in rural Ohio, Miller (1927) remarked upon his delight at finding so many cocoons in a natural environment. Cecropia has also extended its range westward into the plains, coinciding with the movement of settlers (Sweadner, 1937). These observations and our own suggest that the founding of towns with shade trees and shrubs provided habitats that can support much larger cecropia populations than are usually found in wild or rural habitats.

Cecropia is univoltine, overwintering as a diapausing pupa in a tough cocoon firmly attached to the food plant or to a nearby shrub. The emergence curve of the adults is bimodal, with one group emerging in late May and another in late June (Sternburg & Waldbauer, 1969; Waldbauer & Sternburg, 1973; Waldbauer, 1978). The adults do not feed and have an average life span of only about ten days (Rau & Rau, 1914). The larvae feed on a wide variety of woody plants, and spin and pupate in late summer or early fall (Waldbauer & Sternburg, 1967b; Ferguson, 1972; Scarbrough et al., 1974). Cecropia occurs in most of the eastern United States, from southern Canada to the Gulf States and from the east coast to the Rockies (Ferguson, 1972).

STUDY AREAS AND METHODS

During the winters of 1965–66, 1967–68 and 1968–69 we collected cocoons extensively in Champaign Co. Collections were made throughout the contiguous cities of Urbana and Champaign, records being kept by street address so that we could plot distributions. We also collected from the woody plants along 93 km of railroad tracks north and east of Urbana and Champaign, including about 45 linear km of stands of *Salix interior* Rowlee (sandbar willow). Two natural forests, Hart and Trelease Woods, were also searched for cocoons.

The distribution of adult cecropia was surveyed in 1968 and 1969 (Sternburg & Waldbauer, 1969; Scarbrough, 1970) by luring wild males to traps baited with virgin females. Locations of our five traps were: two, 6.8 km apart, in urban residential areas near opposite edges of the Champaign-Urbana metropolitan area, one of them 1.6 km west of the east edge of Urbana in an area of intermediate age and the other 1.6 km east of the west edge of Champaign in a recently built area; three in nearby rural areas, one at the south edge of Trelease Woods, another 45 m into the east edge of Hart Woods, and the last near a stand of sandbar willow on the railroad right-of-way near Mayview (see below for locations). The traps ran continuously from 13 May to 20 July each year, i.e., until about 12 days after the last moth was caught. However, no traps were at Mayview or Hart Woods in 1968. Each trap was constantly baited with two or three newly emerged females that were replaced every third day and kept in cages in the traps, thus preventing mating and assuring continued pheromone release. Traps were checked daily. Males captured for the first time were marked with an identifying number and released in the morning at the trap site where they had been caught (Sternburg & Waldbauer, 1969; Scarbrough, 1970).

Areas Searched

Trelease Woods, 5 km northeast of Urbana and surrounded by cropfields at the time of the study is a 12 hectare remnant of a prairie grove. It is a mixed mesophytic stand with an abundance of sugar maple (*Acer saccharum* Marshall) and hackberry (*Celtis occidentalis* L.), and with an understory dominated by pawpaw (*Asimina triloba* (L.) Dunal) and thornapple (*Crataegus* sp.). Food plants of cecropia commonly found include: wild black cherry (*Prunus serotina* Ehrh.), wild plum (*P. americana* Marsh), smooth sumac (*Rhus glabra* L.), basswood (*Tilia americana* L.), elderberry (*Sambucus canadensis* L.), sandbar willow (*Salix interior* Rowlee), silver maple (*Acer saccharinum* L.) and *Crataegus* sp.

Hart Woods, 6.5 hectares and on the Sangamon River near Mahomet, is well drained, somewhat xeric, and contiguous with a much larger area of bottomland forest. White and black oaks (*Quercus alba* L. and *Q. velutina* Lam.) dominate the upland; red oak (*Q. rubra* L.) occurs on the slopes, and silver maple, one of cecropia's favorite food plants, is abundant on the adjacent bottomland. Wild black cherry and elderberry, both food plants for cecropia, are common in most of the understory.

Railroad rights-of-way, about 4.5 m wide on each side of the tracks, have mostly herbaceous plants, but there are also scattered cecropia food plants, wild black cherries, box-elder maples (*Acer negundo* L.),

red osier dogwoods (*Cornus stolonifera* Michx.) and elderberries. Sandbar willow abounds in low areas, especially near Mayview, a cluster of about a dozen houses nearly 5 km east of Urbana. The tracksides are bordered by field crops or, in a few places, by osage oranges [*Toxylon pomiferum* (Raf.)] hedgerows.

The older sections of Champaign and Urbana, business districts and the adjacent residential areas, were settled in the late 1800's and early 1900's (Smith, 1957). Trees and shrubs in these areas are mostly old and large, except for trees planted after 1953 to replace elms (*Ulmus americana* L.) lost to disease. In aerial photographs of these old areas, the crowns of trees are seen to overlap and largely obscure the roofs of buildings. Both cities have grown constantly since the late 1940's, and residential areas, recently built on treeless farmland, are located at their peripheries. Trees here are often widely spaced and usually small; in aerial photographs the crowns of trees do not overlap the roofs of buildings. Areas of intermediate age with trees and shrubs of moderate size occur between the old and new areas. In aerial photographs most buildings in these areas are but partially obscured by trees.

In addition to a widespread search for cocoons throughout Urbana and Champaign, the six plots (described below) in old and new residential areas were exhaustively searched to obtain the most quantitative measure possible of relative abundance (Scarbrough, 1970).

Comparison of the Woody Plants of Old and New Residential Areas

The food plants available to cecropia in old and new urban residential areas were compared by censusing all woody plants in three sample plots in each of the two types of areas (Scarbrough, 1970). Intermediate areas were not examined. Preliminary observations showed no differences in the trees and shrubs in back and in front of houses. Therefore, each plot consisted of 300 contiguous front yards and the adjacent street-side plantings. Their areas were 22, 15, and 15 hectares, respectively, for plots A, B and C in new neighborhoods; and 13, 14, and 17 hectares, respectively, for plots D, E and F in old neighborhoods. The relative density of each species of woody plant was calculated as:

$$\text{Relative density} = \frac{\text{total number of individuals of one species}}{\text{total number of individuals of all species}} \times 100$$

Predation Studies

Waldbauer & Sternburg (1967a) found that most of the cecropia pupae in cocoons on trees and on the upper branches of shrubs in

Champaign and Urbana had been killed by downy woodpeckers, *Dryobates pubescens* (L.), and hairy woodpeckers, *D. villosus* (L.), during winter. The seasonal progression of predation and whether or not a comparably high level of predation would occur again were determined by observing 250 naturally occurring cocoons in the six plots. These cocoons, left *in situ*, were checked for the easily identified woodpecker damage every two weeks from 12 October to 13 May, when new leaves appeared on the trees (Scarbrough, 1970).

We also attempted to measure the potential extent of woodpecker predation on pupae in woodlands where cecropia cocoons rarely occur. Cocoons with living pupae and still attached to twigs were taped (General Electric plastic electrical tape) to thin pawpaw or wild black cherry saplings 3 to 6 m tall in Trelease and Hart Woods. The saplings were bent down and a cocoon was taped snugly to the trunk or a main branch. When the saplings were relased the cocoons were at heights comparable to those of cocoons in urban areas. To control for the effects of taping, cocoons were similarly placed in an old residential area in Champaign where woodpecker predation was known to occur. They were taped to saplings when possible, but most had to be taped to low branches of large trees. Fifty cocoons were placed one to a tree and not less than 45 m apart in each of the three areas. They were checked for damage every two weeks, beginning on the first of November, until the last cocoon had been attacked (Scarbrough, 1970).

The mice *Peromyscus leucopus* (Rafinesque) and *P. maniculatus* (Wagner) prey extensively on cecropia pupae in trackside and roadside areas, leaving an easily recognized injury (Scarbrough et al., 1972). An experiment similar to the one described above determined the potential predation by these mice on cecropia cocoons in Trelease and Hart Woods. Cocoons still attached to twigs were taped to shrubs or tree sprouts as near the ground as possible, the usual position of wild cocoons attacked by mice. Cocoons to control for the effect of taping were similarly placed in two areas where predation by mice was known to occur, the trackside vegetation near Mayview and a row of *Cornus stolonifera* along Interstate 74 near Champaign. Twenty were placed in each location, one to a bush or tree, about 9 m apart. The cocoons were checked monthly from 15 November to 15 May.

RESULTS

Distribution of Cecropia: Rural vs. Urban Areas

Cocoons were scarce in rural areas (Table 1). None were found in Hart Woods, and only one in Trelease Woods. Ninety-three linear km of trackside vegetation examined in 1968–69 yielded 196 cocoons,

TABLE 1. Numbers of the current year's cocoons of *Hyalophora cecropia* (L.) found in urban and rural areas of Champaign Co., Illinois, and the numbers of *H. cecropia* males caught for the first time in the same areas in traps baited with virgin female *H. cecropia*.

	Rural areas			Urban areas
	Mayview trackside	Hart Woods	Trelease Woods	Champaign and Urbana
Cocoons found				
1967–1968	—	0	0	721
1968–1969	92	0	1	980
Males captured				
1968	—	—	32	1033*
1969	139	14	41	1749

* Data from Sternburg & Waldbauer (1969).

47% (92) from the 6.4 km strip of sandbar willow near Mayview, 39% from other sandbar willow thickets, and 15% from other species of woody plants. Only twelve cocoons with pupal exuviae, and thus, at least one year old, were found at the Mayview site in 1968–69.

Cecropia was, however, abundant in urban areas. In 1967–68 we found 721 cocoons, and in 1968–69 we found 980 within the limits of Urbana and Champaign (Table 1). They were collected only from street sides and front yards. Cocoons in back yards were not disturbed; the males that eventually emerged from them were sampled by means of the traps.

The large number of males caught confirms the abundance of cecropia in this urban area (Table 1). In 1968 there were 1033 previously uncaptured males caught in two traps in the urban area, but only 32 were caught in the one trap at Trelease Woods. Similarly, in 1969 there were 1749 previously uncaptured males caught in two urban traps, but only 194 were caught in three rural traps. Cocoon collections indicated that urban cecropia outnumbered rural cecropia by 5:1; trapping indicated a ratio of 9:1. Trapping is probably the more sensitive sampling method, but it probably overestimated the rural population, because the Mayview trap was near the only known large concentration of rural cecropia cocoons. Nevertheless, the results of the two methods agree fairly closely and leave little doubt that urban cecropia greatly outnumbered rural cecropia.

The rural population may be partly maintained by moths from the urban area. About 12% of the marked males captured at Mayview had been released at Urbana and about 4% at the Champaign trap. About 44% of the marked males captured at Trelease had been released at the Urbana trap (Table 2). Thus, it appears that a significant number

TABLE 2. Sites of release and recapture of male *Hyalophora cecropia* (L.) recaptured in 1969.

Release site	Site of recapture				
	Trelease Woods	Mayview	Hart Woods	Urbana	Champaign
Trelease Woods	6	15	0	0	0
Mayview	3	51	0	1	0
Hart Woods	0	0	2	0	0
Urbana	7	9	0	336	16
Champaign	0	3	0	6	767
Total	16	78	2	343	783

of males, and possibly females, move from the urban to the rural habitat. On the other hand, only one male released at a rural trap was recaptured in the urban area.

Distribution of Cocoons within the Urban Area

The locations of the cocoons collected in all areas of Champaign and Urbana during the winters of 1965–66, 1967–68 and 1968–69 were plotted on separate city maps. Fig. 1 shows that most of the cocoons collected in 1967–68 came from new residential areas at the periphery of the cities, particularly in the southwest quadrant where the most extensive new areas occurred. The maps for 1965–66 and 1968–69 show almost identical distributions (Scarbrough, 1970). Table 3 shows the distribution by old, new and intermediate residential areas of all cocoons found from 1965 to 1969. From 66% to 80% were found in new areas, 16% to 23% in intermediate areas, but only from 4% to 10% in old areas. Furthermore, most of the cocoons from old areas were from sites adjacent to new or intermediate areas.

A more accurate estimate of this differential distribution was obtained by making an exhaustive search for cocoons in the six plots in old and new residential areas during the three winters from 1967 to

TABLE 3. Distribution in old, intermediate, and new residential neighborhoods in Champaign and Urbana of all cocoons of *H. cecropia* collected during three winters.

Neighborhoods	1965–66 Cocoons		1967–68 Cocoons		1968–69 Cocoons	
	No.	%	No.	%	No.	%
Old	47	10.5	47	5.7	42	3.9
Intermediate	103	23.1	145	17.6	172	16.2
New	296	66.3	631	76.6	844	79.8
Total	446		823		1058	

TABLE 4. The number and percentage of cocoons collected in six sample plots in old and new residential areas in Champaign and Urbana in each of three years. Percentages are based on the total number of cocoons collected each year in these plots.

	1967–68 Cocoons		1968–69 Cocoons		1969–70 Cocoons	
Plots	No.	%	No.	%	No.	%
New areas						
A	162	56.8	186	36.7	441	46.0
B	32	11.2	171	33.8	133	13.9
C	69	24.2	129	25.5	330	34.4
	263	92.2	486	96.0	904	94.3
Old areas						
D	4	1.4	4	0.8	17	1.8
E	11	3.8	15	2.9	31	3.2
F	7	2.5	1	0.2	6	0.6
	22	7.7	20	3.9	54	5.6

1970. In these plots well over 90% of the population was concentrated in the new residential areas; from 3.9% to 7.7% occurred in old areas (Table 4). These data are in close agreement with Table 3 where, excluding data from intermediate areas, about 7.1% of the cocoons came from old areas. Cocoons taken in neighboring cities of the county were also found almost exclusively in new residential areas.

Woody Plants of Old and New Residential Areas

There is little difference in the species of trees that are available to cecropia in old or new residential areas (Table 5). Many of them are preferred hosts (Waldbauer & Sternburg, 1967b, and Scarbrough et al., 1974). Although there were some variations between areas, silver maple was overall the most abundant tree. In two of the new residential plots, its relative density was over 26%, averaging 2 trees per hectare. In another new plot, its relative density was only 9%, with 0.4 trees per hectare; in this plot sugar maple was most abundant. Silver maple was also the most abundant tree in old areas, with relative densities of about 20% (2 trees per hectare) except in one plot where sugar maple was more abundant at a relative density of 25%.

The density of all trees, irrespective of species, did not vary much either. In the new areas there were 56.6, 44.4, and 45.2 trees per hectare in plots A, B and C, respectively; in the old areas there were 52.3, 37.7, and 35.2 trees per hectare in plots D, E and F, respectively. A much larger total amount of foliage was available in the old residential areas, because the trees were much larger.

There were no significant differences in the species of shrubs pres-

TABLE 5. The relative density of trees in the six sample plots in old and new neighborhoods of Champaign and Urbana, Illinois.

Tree species	New neighborhoods			Old neighborhoods		
	A	B	C	D	E	F
Acer saccharinum L.	9.0	28.2	26.0	20.2	20.2	13.1
**A. saccharum* Marsh.	3.6	3.2	1.1	12.2	13.0	25.4
A. rubrum L.	8.3	8.4	2.0	1.3	3.8	7.5
**A. platanoides* L.	1.8	1.4	2.8	0.9	4.8	6.7
Prunus spp.	1.8	0.4	1.2	3.6	1.0	2.5
Malus spp.	9.0	6.6	6.4	3.0	3.6	2.5
Crataegus spp.	0.7	2.2	0.0	0.4	0.0	0.0
Betula pendula Roth	4.2	1.4	2.4	1.0	1.2	0.6
B. papyrifera Marsh.	4.7	0.6	5.4	1.0	1.5	0.4
B. populifolia Marsh.	9.7	3.5	5.0	0.3	2.4	1.7
Platanus occidentalis L.	5.0	13.7	15.3	5.4	4.1	5.2
**Liquidambar styraciflua* L.	4.4	3.5	3.2	0.9	0.8	1.0
**Ulmus* spp.	2.2	4.5	1.5	12.1	3.2	0.8
**Celtis occidentalis* L.	0.8	0.0	0.3	4.4	2.4	2.7
Quercus spp.	5.8	3.1	4.0	4.4	10.0	4.2
Fraxinus spp.	4.7	5.7	10.2	9.8	6.8	7.1
Cornus florida L.	2.4	0.8	0.9	0.2	0.4	0.8
Gleditsia triacanthos L.	7.9	2.1	4.6	1.6	3.5	4.4
**Ailanthus altissima* Swin.	0.0	0.0	0.0	4.6	0.6	2.3
Others	14.0	10.4	7.9	12.5	14.0	11.0

* Species on which cecropia seldom or never occurs or on which the survival rate of first instars was found to be abnormally low (Scarbrough et al., 1974).

ent in the six plots. The most common were various species of juniper (*Juniperus* spp.), yew (*Taxus* spp.), spirea (*Spiraea* spp.), and privet (*Ligustrum vulgare* L.). Dense coniferous trees, some shrubby, included various pines (*Pinus* spp.), spruces (*Picea* spp.), and white cedar (*Thuja occidentalis* L.). Many cocoons were found on these plants each year. Previous experiments showed that these plants (except for spirea) are not capable of supporting normal growth by first or fifth-instar cecropia larvae (Scarbrough et al., 1974); thus, the larvae must have migrated to these plants from other plants just before spinning.

Other shrubs that are food plants for cecropia occurred sporadically in the sample plots, including lilac (*Syringa vulgaris* L.), cotoneaster (*Cotoneaster* spp.), tall hedge (*Rhamnus frangula* L.) and red-osier dogwood. Their densities were low, but they frequently harbored cocoons.

Although old and new residential areas did not differ much in the density or species composition of their woody vegetation, there were major differences in the age of the trees and in the proximity of shrubs to trees, the latter due to a change of fashion in landscaping. In new areas the trees were young, between 2 and 10 m tall, and often located

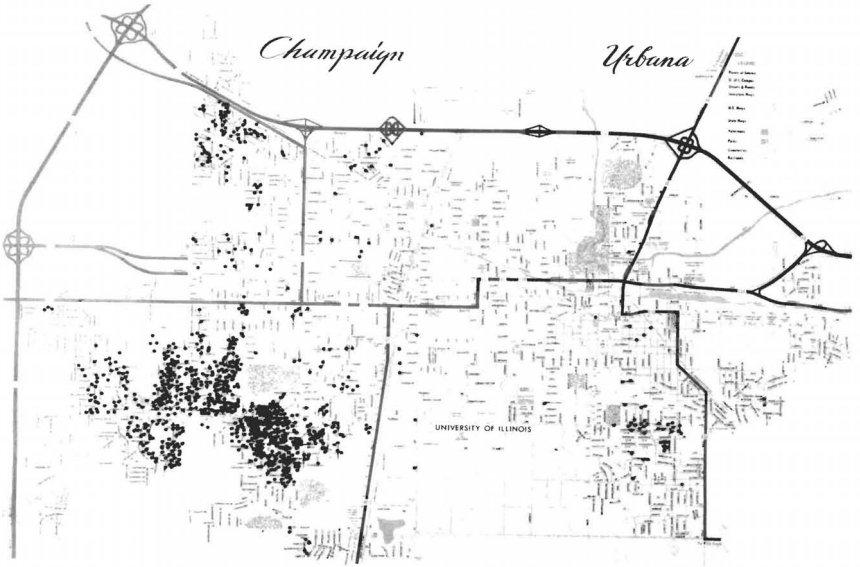

FIG. 1. The distribution of the cocoons of *Hyalophora cecropia* found in Champaign and Urbana in 1967–68.

near the center of a lawn within a few meters of shrubs or with shrubs at their base. The proximity of shrubs to host trees probably increases the survival of migrating larvae by providing nearby safe sites for cocoon spinning (Scarbrough et al., 1977). In old areas the trees were very large, usually at least 20 m tall, and generally located along the margins of lawns and streets. Shrubs and trees were generally farther apart than they were in new areas.

Predation Studies

The seasonal progression of woodpecker predation on 250 cocoons in urban trees is shown in Fig. 2. Predation began shortly before the leaves began to drop in the fall. The first cocoons attacked were not concealed by leaves but were exposed on the trunk or on short spurs originating from the trunk. At this early date, cocoons on twigs and branches were still hidden by leaves and apparently not visible to woodpeckers.

The rapid rise in predation rate coincided with leaf fall, which began in the last week of October. Most leaves had fallen by mid-November and the trees were almost completely bare by the beginning of December. The rate of woodpecker attacks remained fairly constant through most of the winter and declined in early spring; the attacks had stopped by 29 April. The decline was no doubt due to the in-

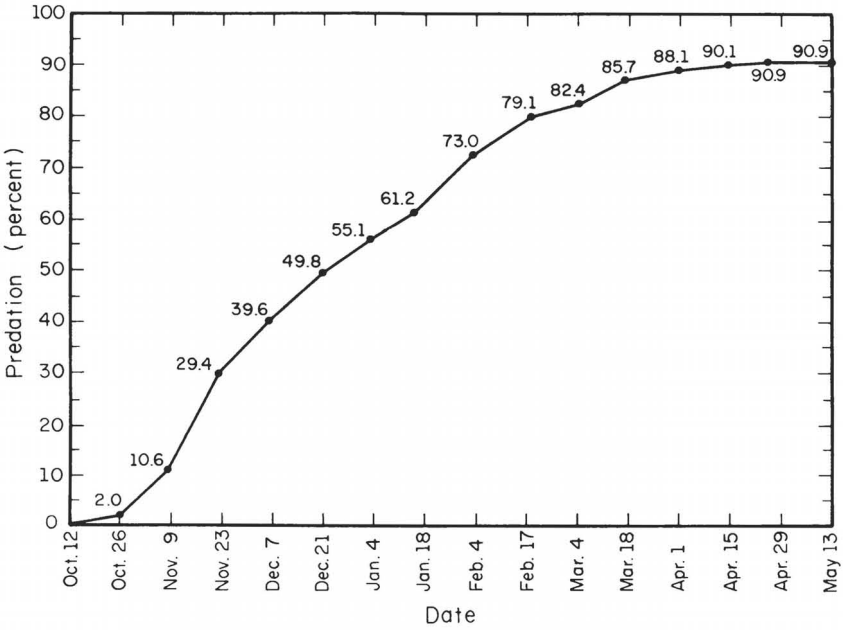

FIG. 2. The rate and seasonal progression of predation by woodpeckers on a group of 250 naturally occurring cocoons of *Hyalophora cecropia* on the branches of trees in urban residential areas of Champaign and Urbana in 1969–70.

creased difficulty the birds had in locating the few remaining unattacked cocoons. Almost 91% of the cocoons under observation were successfully attacked by woodpeckers, which agrees closely with the observation by Waldbauer & Sternburg (1967a) that 86.5% of the cocoons in trees had been attacked. Cocoons spun in evergreen shrubs or near ground level in deciduous shrubs or suckers at the bases of trees were virtually exempt from predation by woodpeckers.

Only two of the cocoons taped high in woodland trees were attacked by woodpeckers, one each at Trelease and Hart Woods. In addition, one naturally occurring cocoon attacked by a woodpecker was found at Trelease Woods. Woodpecker attacks on taped cocoons, as well as the other attacks mentioned below, occurred some time between the last week of December and 21 January. Woodpecker predation on the control cocoons taped to trees in old urban areas began much earlier and had reached 78% by 21 January. Downy and hairy woodpeckers are common in both Trelease and Hart Woods, as well as in both old and new urban areas. (Downy woodpeckers also occur in the trackside and roadside areas.) It seems likely that the forest-dwelling woodpeckers were slow to attack the taped-up cocoons, because they had

had little or no previous experience with cecropia cocoons. Whether or not the woodland woodpeckers would eventually have attacked more cocoons is not known, because the remaining 98 cocoons were destroyed by some unidentified predator at about the same time that the woodpecker attacks began.

The injury left by this unidentified predator(s) resembles neither woodpecker injury (Waldbauer et al., 1970) nor mouse (*Peromyscus* spp.) injury (Scarbrough et al., 1972). (As judged by the injury, all attacks on cocoons in the urban area had been by woodpeckers.) The holes in most of the cocoons attacked by unidentified predators were nearly 2 cm long and 0.5 cm wide. A few had long narrow slits 3 to 4 cm long. Most of these cocoons had been ripped open rather than chewed, abraded, or punctured. Sometimes, loose silk remained on them, but it had been pulled outward rather than pushed inward as is the case with woodpecker attacks. The entire pupa had been removed from each of these 98 cocoons—apparently in one piece, because the cocoons were not stained by the semi-liquid pupal contents that would have leaked out if the pupae had been pierced or broken into pieces. This seems to eliminate birds from consideration, since it is difficult to see how they could remove a large pupa through such a small hole without breaking it or at least piercing it.

The animal(s) most likely to be responsible are the fox squirrel, *Sciurus niger* L., gray squirrel, *S. carolinensis* Gmelin, and flying squirrel, *Glaucomys volans* (L.). They could rip the cocoons open with their incisors and remove the pupae with their front paws. According to Martin et al. (1951), gray squirrels eat pupae from unspecified cocoons and fox squirrels eat Lepidoptera of all stages. Both gray and flying squirrels are absent from Trelease Woods, but fox squirrels occur at both Trelease and Hart Woods (Lonnie Hansen, Illinois Natural History Survey, Urbana 61801, personal communication). Both fox and gray squirrels occur in Champaign and Urbana, but we have not found cocoons that bear this type of injury in the urban area. However, squirrels are almost confined to old or intermediate residential areas where cecropia cocoons are relatively scarce.

The cocoons taped to the bases of woody plants at Trelease and Hart Woods were almost ignored by mice, and none were attacked by other predators; two were opened by mice at Trelease and none at Hart Woods. On the other hand, similarly treated cocoons placed in rural areas where cecropia cocoons occur naturally were heavily attacked. Mice opened 65% of those taped to willows at Mayview and 40% of those taped to dogwood shrubs along Interstate 74. *Peromyscus leucopus* occurs both in the woods and in these other areas. We believe that woodland *P. leucopus* seldom attacked the taped cocoons,

because, like woodland woodpeckers, they had had no previous experience with cecropia cocoons. This view is supported by the finding of Scarbrough et al. (1972) that, in the laboratory, *P. leucopus* that had been trapped at a site where cecropia cocoons were abundant attacked and opened cecropia cocoons much more readily than did *P. leucopus* that had been trapped at Trelease Woods.

Each year we find in the urban area several dozen cocoons with various kinds of seeds, sometimes whole acorns, stuffed into their valves. We do not know how frequently this causes mortality, but on at least one occasion it blocked the emergence of an adult, causing its death. The responsible animal has not been identified, but it is probably the blue jay, *Cyanocitta cristata* L. (Waldbauer & Sternburg, 1976).

DISCUSSION

The local distribution of cecropia described above raises three obvious questions: 1) Why are they abundant in some urban environments and scarce in rural environments? 2) Why, in rural areas, are they virtually absent from forests but present, although in small numbers, in short trackside and roadside woody vegetation? 3) Why are they abundant in new urban residential areas but very scarce in old urban residential areas?

Old urban residential areas and forests both have characteristics of a climax, at least in that their woody vegetation consists largely of mature trees and shrubs. On the other hand, new urban residential areas and stands of small willows and other woody plants along railroad tracks and roads resemble an early stage in the succession. Thus, the fundamental question may be why cecropia is more abundant in early stages of the succession than in the climax. We have found what we believe to be a major reason for the difference in numbers of cecropia in urban and rural areas, but our discussion of the remaining questions is based largely on circumstantial evidence.

No doubt, a complex of factors is responsible for the greater abundance of cecropia in new urban areas than in rural areas (Table 1), but so far we have concrete evidence of only one such factor, a large difference in the predation pressure on the pupae in winter. In rural areas only about 29% of the overwintering pupae survived, but in the urban area about 66% of them survived (Waldbauer & Sternburg, 1967a; Scarbrough, 1970; Scarbrough et al., 1977). In both urban and rural areas, at least 90% of the pupae in cocoons that were exposed above the ground litter were killed by woodpeckers; this comes to about 6% of the pupae in the trackside vegetation at Mayview and about 20% of those in the urban area. However, in rural areas cocoons

spun near the ground (usually over 90%) are heavily attacked by mice, while cocoons spun near ground level in urban areas (about 80%) are virtually exempt from attack of any kind. During two winters at Mayview, at least 62% of all cecropia cocoons were destroyed by mice, while in the urban area we have seen only three cocoons that were destroyed by mice out of several thousand that we have collected since 1965 (Waldbauer & Sternburg, 1967a; Waldbauer et al., 1970; Scarbrough et al., 1972). This 62% mortality includes cocoons that were opened where they had been spun (57.1%), plus others that were removed from the spinning site (4.8%). There is no doubt that the cocoons *in situ* had been opened by *Peromyscus* spp. (Scarbrough et al., 1972), and the removal of cocoons can probably also be attributed to *Peromyscus* spp. Four cecropia cocoons and a *Peromyscus* nest were found next to each other under a log near Urbana; three of these cocoons had been opened (they bore the characteristic mouse injury), and one still contained a pupa (personal communication from Lloyd Davis, Dept. of Entomology and Nematology, University of Florida, Gainesville 32611). It may well be that considerably more than 62% of the cocoons at Mayview were destroyed by mice; we probably did not account for more than a few of the cocoons that had been removed, because the scraps of silk that are left behind are very difficult to find.

The reason for this striking difference in predation pressure is a difference in the feeding behavior of the species of mice that inhabit rural and urban areas. Extensive trapping showed that the native wild mice *Peromyscus leucopus* and *P. maniculatus* are almost absent from both new and old urban residential areas, but that the house mouse, *Mus musculus* L., is common there, constituting over 91% of the small mammals trapped on front lawns. In the urban area we caught *Peromyscus* spp. only near stream banks or other intrusions of rural habitat. In rural areas the situation was reversed; over 89% of the small mammals caught were *Peromyscus* spp., but only 7.4% were *M. musculus*. In the laboratory *M. musculus* ate naked cecropia pupae and incorporated silk from the cocoons in their nests, but under no circumstances did they open a cocoon to obtain a pupa. On the other hand, in the laboratory all *P. leucopus* and most *P. maniculatus* readily opened cecropia cocoons and ate the pupae (Scarbrough et al., 1972).

We have less information on why cecropia is over thirteen times more abundant in new urban residential areas than in old urban residential areas (Table 3). It is very likely that cecropia follows a pattern that evolved long before Europeans came to the New World and built urban areas—that it is a "fugitive species" (Hutchinson, 1951) whose

population is constantly shifting to areas early in the succession. This is borne out by our observations over the past fifteen years. From 1965 to 1980 there has been a major shift in the location of the cecropia population in Champaign and Urbana. Residential areas that were new in 1965 now have much larger trees and produce very few cecropia cocoons, but other areas that were crop fields in 1965 have since become new residential areas that now produce many cocoons. Cecropia thus does seem to be a fugitive species that constantly "flees" to areas early in the urban succession. This pattern of scarcity in climax communities also seems to hold true in rural areas; as we saw above, cecropia was almost absent from woodlands, but occurred in small numbers in the early successional communities found along roads and railroad tracks (Table 1). We do find occasional cecropia larvae in the woodlands, but we have found only one cocoon there. Obviously, some oviposition occurs in the woodlands, but cecropia does not often survive past the larval stage there, suggesting that the population differences between early and late successional stages might be due to mortality that occurs before the pupal stage, probably in the larval stage.

Although we label cecropia a fugitive species, there still remains the question of what there is about the woodland climax or the "urban climax" that causes the cecropia population to be so low there. A lack of suitable food plant species cannot be responsible, because the same species of woody plants are about equally abundant in new and old urban areas (Table 5), and because the rural woodlands, tracksides and roadsides all have plant species that are often used as hosts by wild cecropia in this area. Woodlands and old urban areas might be discriminated against because of some direct response of cecropia to the size of the trees. For example, the females might prefer to oviposit on small trees. Another, and perhaps more likely, possibility is that cecropia are less likely to survive in woodlands and old urban residential areas because of a higher rate of predation and/or parasitization on the larvae.

We do have circumstantial evidence which suggests that predation by birds on the larvae may be a major reason for the paucity of overwintering cecropia in old residential areas. The new areas, built on former crop fields and lacking large woody plants, have a bird fauna that is very different from that of the old areas with their large trees and shrubs. Our own observations leave no doubt that ground-frequenting birds are common in the new areas. However, birds that search woody plants for caterpillars, although abundant in old areas, are relatively scarce in new areas. These are blue jays, brown thrashers (*Toxostoma rufum*), catbirds (*Dumetella carolinensis*), mockingbirds (*Mimus polyglottos*) and cardinals (*Richmondena cardinalis*).

We have seen all of these species prey on cecropia caterpillars in the field. Graber & Graber (1963) list all of the above mentioned species, except the mockingbird, as common residents of urban residential areas of central Illinois. However, we have seen mockingbirds in old residential areas of Champaign and Urbana on many occasions. Graber & Graber (1963) do not specify whether their data apply to old or new residential areas, but R. R. Graber (Illinois Natural History Survey, Urbana 61801, personal communication) told us that their data came almost entirely from old residential areas and that mockingbirds are common in old areas. The situation is similar in rural areas. Foliage-gleaning birds are abundant in the woodlands, especially at the edges where cecropia food plants are most abundant, but these birds are very scarce in the trackside and roadside areas.

Cecropia is attacked by several parasitoids (Marsh, 1937), but they cannot be responsible for the observed differences in cecropia population size between rural and urban areas or between old and new urban areas. Until 1975 less than 1% of the cocoons from Champaign Co. contained parasitoids. In 1975 about 5% of the cecropia cocoons in one small area of the city of Champaign contained cocoons of *Enicospylus americanus* (Christ) (Hymenoptera: Ichneumonidae). This parasitoid was relatively common and widespread in Champaign and Urbana in 1979–80, but was very uncommon in 1980–81. We have found a few cocoons containing larvae that had apparently died of disease, but we know nothing of the incidence of death in younger larvae due either to disease or parasitism.

Cecropia must be highly mobile to locate early successional areas so rapidly. Nothing is known of how far the females fly, but it is known that the males are often caught from 6.8 to 12.5 km away from the release point in traps baited with virgin females (Sternburg & Waldbauer, J. Lepid. Soc., in press).

The list of cecropia's preferred food plants (Scarbrough et al., 1974 and references therein) supports the idea that cecropia is essentially a species of the early stages of succession. Included on this list are such early successional plants as the poplars (*Populus* spp.), willows (*Salix* spp.), thorn apples (*Crataegus* spp.), wild black cherry, staghorn sumac (*Rhus typhina* L.), silver maple, box elder maple and the birches (*Betula* spp.). Even in the urban environment 54.2% of the cocoons found on food plants were found on plants included on the preceding list.

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