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SELECTION OF THE COCOON SPINNING SITE BY THE LARVAE OF *HYALOPHORA CECROPIA* (SATURNIIDAE)¹

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The univoltine *Hyalophora cecropia* (L.) overwinters as a diapausing pupa in a silken cocoon that is usually anchored to a woody plant. Some are well above ground level on the branches of deciduous trees or shrubs, but most are near the ground among the stems of deciduous shrubs, among adventitious shoots at the base of a deciduous tree, or on an evergreen shrub. After leaf fall, cocoons on bare branches are clearly visible. Cocoons near ground level are usually hidden by grass, debris, or evergreen foliage.

The location of a cocoon significantly affects the probability that it will be found by a vertebrate predator during the winter, and largely determines the species of predator that will find it. In residential areas of Champaign and Urbana, Illinois, from 86.5%–90.9% of the high cocoons were destroyed by woodpeckers, while cocoons low in shrubs or shoots were almost exempt from predation (Waldbauer & Sternburg, 1967b; Waldbauer et al., 1970; Scarbrough, 1970). In rural habitats, not only are most pupae in cocoons on bare branches killed by woodpeckers, but those near ground level may be killed, although less frequently, by mice of two species, *Peromyscus leucopus noveboracensis* (Fisher) and *P. maniculatus bairdii* (Hoy & Kennicott), which do not occur in urban and suburban areas (Scarbrough et al., 1972) (see also Marsh, 1937).

There is little literature on the behavior which leads to the selection of a spinning site by cecropia, no quantitative data on whether or not the larvae migrate from the food plant before spinning, on the extent of migrations, and on whether or not the migrations are affected by the

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growth form of the host plant. We examined the behavior of cecropia larvae during the period which begins with the cessation of feeding and ends with the beginning of spinning. We are particularly concerned with the effects of the environment, especially plantings in urban and suburban residential areas, where cecropia is most abundant in central Illinois.

Cecropia larvae feed on many species of deciduous plants, almost all woody and including both shrubs and trees (Ferguson, 1972; Scarbrough et al., 1974). Feeding larvae are relatively sedentary and seldom leave the host plant (unpublished observations). Cocoons may be anchored to shrubs or trees which are known hosts of cecropia, but a significant number is found on plants, usually shrubs, which are not eaten by cecropia larvae (Waldbauer & Sternburg, 1967a; Scarbrough et al., 1974), indicating that some larvae leave the host plant before spinning.

MATERIALS, METHODS, AND RESULTS

The larvae used in these experiments, progeny of locally collected pupae, were reared outdoors under nets on *Malus pumila* Mill. (apple), *Prunus serotina* Ehrh. (wild black cherry), *Acer saccharinum* L. (silver maple), or *Cornus stolonifera* Michx. or *C. alba* L. (shrubby dogwoods) as described by Waldbauer & Sternburg (1973). Experiments and sampling were done on the University of Illinois campus or residential areas in Champaign and Urbana, Illinois.

Larvae transferred to trees or shrubs were always fifth instars which would continue to feed for at least four or five days before wandering off to spin their cocoons. They almost invariably completed the feeding phase within a few feet of the twig to which they had been transferred.

Expt. I. Emptying the gut and moving to the spinning site.

Feeding larvae reared on apple, silver maple or wild black cherry were transferred for observation to an unnetted tree of the same species, with no shoots at its base. They were placed singly on branch tips at the outer edge of the crown. Each morning they were counted and then watched continuously from 0500–1900 hours. We recorded relevant behavior and the time at which it occurred. At the end of the day larvae which had left the tree were replaced with new larvae.

Mature larvae emptied the gut before moving to a cocoon spinning site, clinging from the underside of a branch by the thoracic legs and the first two or three pairs of prolegs, and allowing the end of the abdomen to hang free. They first passed dry, black feces, then progressively softer greenish feces, and finally a transparent, gelatinous liquid. When finished they crawled away on the upper side of the branch.

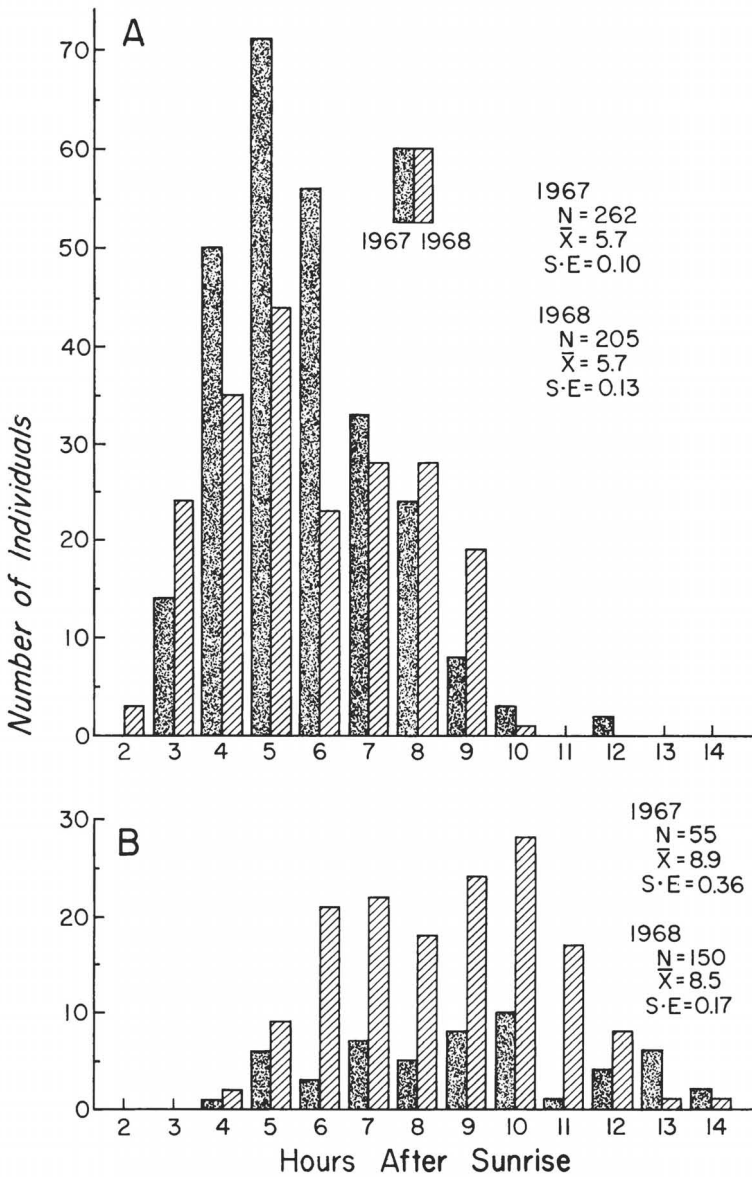


Fig. 1. The times at which cecropia larvae began to empty their guts (A) and the times at which they began to spin the cocoon (B). Times have been rounded off to the nearest hour after sunrise.

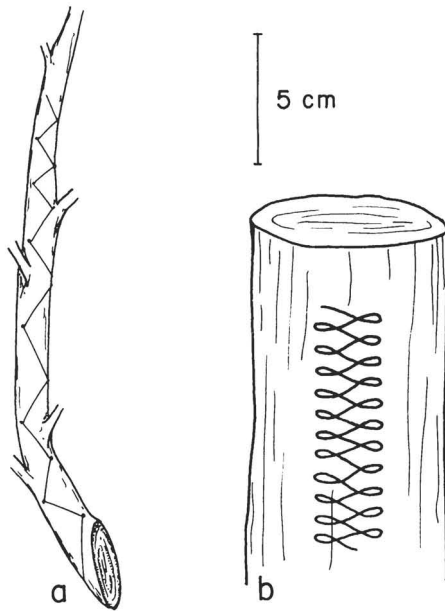


Fig. 2. Diagrammatic representation of the trails of silk left by wandering cecropia larvae on a thin branch (a) and a wide branch or trunk (b).

Gut emptying always occurred during daylight, most larvae beginning between 3 and 9 hours after sunrise, the mean being 5.7 hours after sunrise in both 1967 and 1968 (Fig. 1A). The process required from 15–130 minutes, a mean and S.D. of 38 ± 19 .

After emptying their guts, they quickly moved to the trunk and crawled downward, often diverging onto side branches, but usually returning to the trunk and the downward path. Some spun in the tree (see below), but most descended to the ground.

They swung the head and thorax from side to side as they crawled, leaving a zig-zag trail consisting of a single strand of silk (Fig. 2). This motion is similar to the “swing-swing” reported as a component of cocoon construction, but not of crawling, by van der Kloot & Williams (1953a, b). On very small branches or rough bark the larvae obtained a secure hold and crawled rapidly, leaving a spread-out pattern (Fig. 2a). On larger branches with smooth bark they crawled slowly and left a compressed pattern (Fig. 2b). Ten larvae timed on a 1 cm diameter branch crawled at a mean rate of 78.0 cm per minute, while 10 others, timed on a smooth-barked branch 5 cm in diameter, crawled at a mean rate of 3.0 cm per minute.

Larvae descending large, smooth-barked branches or trunks, often paused at small branches or areas of rough bark, continuing to deposit silk with the swing-swing movement, and sometimes pausing long enough to form a thin sheet of silk. Although we did not see it happen, this might lead to the spinning of a cocoon. Indeed, in a sample of 323 cocoons from small silver maples or birches (not including cocoons from shoots at the bases of the trees), 26% had been spun on small patches of rough bark or at the base of small branches on the predominantly smooth-barked trunk and large branches.

Fig. 1B includes larvae that left the tree in search of a spinning site. Their wandering phase usually lasted from less than an hour to 8 hours; mean \pm S.D. were 3.8 ± 1.8 hours in 1967 and 3.2 ± 1.3 hours in 1968. They began to spin cocoons from 4–14 hours after sunrise, the means being 8.9 and 8.5 hours after sunrise in 1967 and 1968 respectively (Fig. 1B). Spinning usually began on the same day the gut was emptied, but on a few unusually cool days migrating larvae rested on a woody plant from late afternoon until they resumed wandering the following day.

We found, as did van der Kloot & Williams (1953a), that wandering larvae often pass locations which appear to be suitable for cocoon construction. This was exemplified by 40 larvae of Expt. IV that we timed after they had descended a tree with many adventitious shoots at its base. They eventually spun among these shoots, but first spent from 15–215 minutes ($\bar{x} = 70$) crawling among them. The wandering phase and the cocoon construction phase blend into each other since both involve the deposition of silk.

Expt. II. Selection of the spinning site by larvae feeding in shrubs.

We used 5 sites of two types. Two sites were single shrubs of *Cornus stolonifera* on mowed lawns and at least 10 m from any other woody plant. Three sites were rows of 70 or more contiguous, alternating *C. stolonifera* and *C. alba* on lawns. In one of these rows *Viburnum* sp. and *Malus* sp. were regularly interspersed.

About once a week 5 feeding fifth instars, reared on one of the two species of *Cornus*, were released in each isolated shrub and at four widely separated points in each row. The larvae were marked with a distinctive color for each release point. The following October all cocoons were collected from these sites and their locations noted. The release point of the larva which spun each cocoon was determined by eluting in xylol the marker color from the exuviae in the cocoon (Scarborough et al., 1970).

Sixty larvae were released on the isolated shrubs, but 2 were found dead. Cocoons of 51 (88%) of the survivors were found on the shrubs

TABLE 1. Location of cocoons of *Hyalophora cecropia* collected within a 9 m radius of host trees in residential areas of Champaign and Urbana, Ill. (Expt. III).

Location	Cocoons collected:							
	1967-1968		1968-1969		1969-1970		Total	
	No.	%	No.	%	No.	%	No.	%
Grass or shoots at trunk base	45	14.8	137	17.2	254	36.5	436	24.3
Shrubs	148	48.8	343	43.1	242	34.8	733	40.8
Total not in trees	193	63.7	480	60.4	496	71.3	1,169	65.2
Total in trees	110	36.3	315	39.6	200	28.7	625	34.8

on which they had been released. One of the 7 missing cocoons was at the base of a tree about 9 m away, but the other 6 were not found. Ninety larvae were released in the rows of shrubs. All of their cocoons were found and identified. Only 9% had left the row to spin on nearby shrubs or trees. Thirteen percent spun on the same shrub on which they had been released, 62% on a shrub within 4.6 m in the row, and 16% on a more distant shrub in the row.

The fact that these larvae spun near the release site does not mean that they did not wander just before spinning. We watched some of them, and they crawled about at the base of the shrubs for a long time. The shrubs afford ample shade and the numerous closely-spaced stems provide a multitude of potential spinning sites. Thus, negative phototaxis and positive thigmotaxis probably kept the wandering larvae in the cover of the shrubs. If they did wander away, they were probably led back by a visual response to the silhouette of the shrub (see Expt. VI). Indeed, two marked larvae were seen returning to the isolated shrub on which they had fed.

Expt. III. The proportion of larvae which leave the host tree to spin.

We estimated this proportion by searching for wild cocoons in plantings on lawns with host trees for cecropia that were relatively isolated from other trees, but were near shrubs which cecropia larvae do not eat (Scarborough et al., 1974). All plants and structures within 9 m of the tree were searched for cocoons. The number and location of the shrubs varied, but in most cases there were from 1-3 shrubs within 2 or 3 m of the tree. From past experience we knew that in similar situations few cocoons are found more than 9 m from the host tree.

Less than 35% of the cocoons were on the branches of the host tree, but over 65% were on adventitious shoots or tall grass at the base of its

TABLE 2. Number and percent of *Hyalophora cecropia* larvae which spun cocoons in trees with two different growth forms after feeding in these trees at different heights above the ground (Expt. IV).

Foliage type	Height of larvae (m)	No. larvae	Larvae which:			
			Spun in tree		Left tree	
			No.	%	No.	%
Dense canopy & drooping branches	3	40	7	17.5	33	82.5
	6	40	9	22.5	31	77.5
	9	40	17	42.5	23	57.5
	Total	120	33	(27.5%)	87	(72.5%)
Thin canopy & horizontal branches	3	40	10	25.0	30	75.0
	6	40	12	30.0	28	70.0
	9	40	13	32.5	27	67.5
	Total	120	35	(29.2%)	85	(70.8%)

trunk, or on shrubs within 9 m (Table 1). The proportion of cocoons found off the trees is a little lower than might be suggested by the results of Expt. IV (Table 2). This probably reflects differences in sampling techniques. In Expt. IV we accounted for all larvae as they left the trees. However, counting cocoons in the sampling areas probably underestimated the number of larvae which left the trees because cocoons are easier to find in trees than in shrubs, because some larvae probably spun beyond the 9 m limit, and because some wandering larvae were probably killed before they spun a cocoon.

Adventitious shoots at the base of the host tree are the preferred spinning site of larvae which migrate from trees. In sample areas where such shoots were present, 83.3% of the cocoons found off the tree were on them. Where the host tree had no basal shoots, 13.1% of the cocoons off the tree were in tufts of grass at the base of the trunk; the remainder were in nearby shrubs.

Expt. IV. Effect on cocoon site selection of the tree's growth form and the height at which the larvae feed.

We used two isolated silver maples on lawns. Both were about 12 m tall and had trunks extending about 2.4 m from the ground to the bases of the bottom branches. One had dense foliage, numerous drooping branches which shaded the trunk and ground all day, and adventitious shoots at the base of the trunk. The other had sparse foliage and relatively few branches, which were mostly horizontal; the trunk and several major branches received direct sunlight; there were no basal shoots.

Feeding fifth instars reared on silver maple were placed in these trees at heights of 3, 6, or 9 m after being marked with a color indicating the height. Y-shaped twigs with the larvae clinging to them were hung in the tree with a long cane pole. The larvae crawled to the leafy tip of a nearby branch (at approximately the intended height) and fed there until they moved to the spinning site. No more than 5 larvae were ever at the same height on one tree at the same time. During daylight the larvae were watched almost continuously, and the number with each color marking that left the tree was noted.

The number of larvae which remained in the trees to spin, 27.5% on one and 29.2% on the other (Table 2), did not differ significantly. However, on the tree with a dense canopy and drooping branches, the greater the height at which the larvae had been placed, the less likely they were to leave the tree ($\chi^2 = 7.02$, $P < 0.05$), while on the tree with a sparse canopy and horizontal branches, their height did not significantly affect the probability that they would leave the tree to spin ($\chi^2 = 0.56$, $P > 0.975$) (Table 2).

Almost all larvae which remained in the trees spun low in the crown, near where the lower branches join the trunk, no matter at what height they had been placed. We found a similar distribution in a sample of 404 wild cocoons collected from the branches of trees during the winter of 1968-69. Ninety-seven percent were within a spherical volume with a 2 m radius that centered on the point where the trunk and lower branches join. Seventy-eight percent were within a concentric volume with only a 1 m radius. The lower portion of these volumes included drooping branches.

The results of Expt. IV raise the question of why high larvae were less likely than low larvae to leave the densely foliated tree, but not the sparsely foliated tree. Van der Kloot & Williams (1953a) postulated that during the wandering phase some internal event must occur before the larva can begin cocoon construction. The occurrence of this event may be a function of time or metabolic or hormonal processes. Larvae which reached the lower crown from the highest release point had expended more time and effort in wandering than the others, and, therefore, were presumably more internally motivated to stop wandering and spin a cocoon. We suggest that the summation of two factors, internal motivation and satisfaction of the larvae's spinning requirements, was more likely to end the wandering phase in the densely foliated tree than in the sparsely foliated tree, perhaps because the larvae are negatively phototactic.

As in Expt. III, shoots at the base of the host tree were the preferred spinning site. Eighty-four of 87 larvae (96.5%) spun among the shoots at

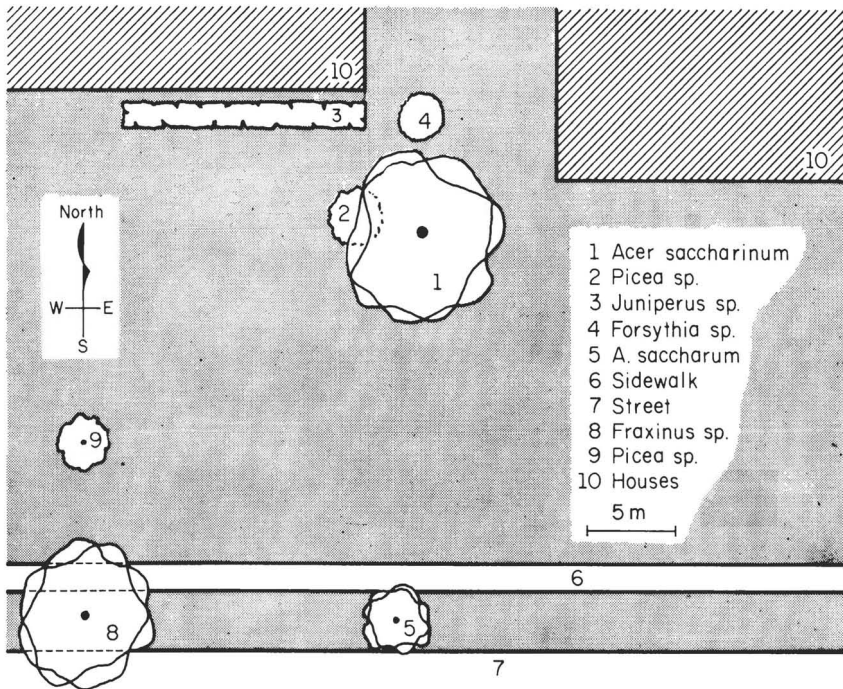


Fig. 3. Diagram of the site of Expt. V, showing residential plantings.

the base of the tree which had them, but only 6 of 85 larvae (6.9%) spun in tufts of grass at the base of the other tree.

Expt. V. Distance from the host tree to the spinning site.

The experimental area was a closely mowed lawn with a silver maple and a number of other shrubs and trees at distances of from 3 m to 23 m from the base of its trunk (Fig. 3). There were no adventitious shoots or tall grass at the base of the silver maple. Eight groups of 10 feeding fifth instar larvae, reared on silver maple, were placed on the lower branches of the silver maple at 6-day intervals. The larvae were marked as described above. They were watched continuously during daylight, and the behavior and route of each migrating larva were recorded.

All larvae left the tree, although two eventually returned to spin on its branches. Seventy-five percent moved more or less directly to the closest spinning site, a spruce (*Picea* sp.) about 3 m from the base of the trunk (Fig. 3). Most of the others moved in the general direction of other shrubs, turning directly toward them when they came within about 1 m.

TABLE 3. Spinning sites chosen by *Hyalophora cecropia* larvae which left the host tree (*A. saccharinum*) (Expt. V). See Fig. 3 for code numbers and locations of the spinning sites.

Spinning site	Meters from trunk of host tree	Larvae spinning:	
		No.	%
<i>Acer saccharinum</i> (1)	0	2 ^a	2.6
<i>Picea</i> sp. (2)	1.2	43	55.8
<i>Forsythia</i> sp. (4)	2.4	5	6.5
<i>Juniperus</i> sp. (3)	3.0	17	22.1
<i>Picea</i> sp. (9)	10.0	2	2.6
<i>Fraxinus</i> sp. (8)	13.7	6	7.8
<i>A. saccharum</i> (5)	9.8	0	0
House (10)	—	2	2.6
Total		77 ^b	

^a These larvae left the tree and returned.

^b Does not include 3 larvae which left the experimental area.

A few moved toward the southeast where there were no shrubs; after moving about 2.5 m from the trunk they turned either north toward the house or south toward the closest tree.

Over 84% of the larvae spun on one of the three woody plants closest to the tree, 56% on the small spruce, the closest spinning site (Table 3). Only 3 left the experimental area. They crawled into the street and were lost.

Expt. VI. Spinning site selection by larvae in trees with no other spinning sites nearby.

The experimental site was a closely mowed lawn with a silver maple 46 m from the nearest other woody plant. There were no shoots or tall grass at the base of the tree. Eighty marked fifth instars that would continue to feed for several days were released and observed as described in Expt. V.

All 80 larvae left the tree. However, 73 of them (91.3%) eventually returned to spin on its branches. Six others climbed trees about 46 m away and spun on their branches. The remaining larva crawled about 37 m to the street and was lost.

They crawled in a more or less straight line away from the trunk of the host tree, occasionally stopping to wave the head and thorax from side to side as if they were trying to get a visual fix on some object. They crawled from 1–25 m ($\bar{x} = 9.5$ m) before returning to the tree. They always took a somewhat different path on the way back, indicating that they did not follow a silk or an odor trail, and suggesting that they used visual cues to orient to the tree.

TABLE 4. Response of wandering *Hyalophora cecropia* larvae to black or white models presented either alone or simultaneously (Expt. VII).

Models presented	No. larvae tested	Larvae moving to:			
		Black model		White model	
		No.	%	No.	%
Black alone	40	36	90.0	—	—
White alone	40	—	—	29	72.5
Black & white simultaneously	40	34	85.0	5	12.5

Expt. VII. Orientation of migrating larvae to models.

We tested the possibility that migrating larvae visually orient to tree trunks or shrubs, determining their responses to flat cardboard models which approximated the silhouette of a low juniper shrub. They were 0.9×1.5 m rectangles painted either white or flat black. We tested 120 larvae which had been placed in an isolated tree on an otherwise bare lawn a few days before the end of the feeding phase. They were tested only after they left the tree spontaneously. After a larva had crawled about 3 m from the tree, a model or a pair of models side by side, was placed a few meters ahead of the larva, parallel to, and about 1 m to the side of its anticipated path. The experiments were done on sunny days with the models placed so that their shadows were cast away from the larvae.

The response of the larvae (Table 4) leaves no doubt that visual cues are an important component in finding spinning sites. There was a strong response to either the black or white model presented alone, although fewer larvae went to the white model. When black and white models were presented simultaneously, 97.5% of the larvae responded, 85% going to the black model.

Positive responses usually consisted of abrupt changes in direction, the larva usually moving to the edge rather than the center of the model. If a model was moved while a larva was approaching, the larva stopped, raised the forward portion of its body, waved from side to side, and then moved toward the new position of the model. All larvae followed the model if it was moved, but some made gradual rather than abrupt turns toward its new position.

DISCUSSION

Our data and the data of Waldbauer & Sternburg (1967a) and Scarbrough et al. (1974) show that, generally speaking, overwintering

cecropia cocoons occur in two sorts of situations: 1) exposed to view on the branches of deciduous trees or shrubs, or 2) hidden near ground level among shoots or the stems of a shrub. The behavior involved in the selection of these sites is especially interesting because exposed cocoons are much more likely to be destroyed by woodpeckers than are hidden cocoons (Waldbauer & Sternburg, 1967b; Waldbauer et al., 1970).

The selection of the spinning site is significantly affected by the immediate environment of the feeding larva. Since feeding larvae are sedentary, we can assume that their location was ultimately determined by the ovipositing female. Larvae which feed on shrubs almost always spin the cocoon close to the ground on the same or an adjoining shrub. Larvae which feed in trees may spin on a branch of the tree, or they may leave and spin near ground level. They rarely return to a tree or climb another tree to spin unless other spinning sites are absent. In suburban, residential plantings, an average of 65%–71% of the larvae in trees ultimately left the tree to spin, either at its base or a more distant site.

The onset of site selection is obviously controlled by a circadian rhythm. The cocoon site is always selected in daylight. Larvae usually begin to wander in the morning and usually begin to spin before nightfall. If not, they rest during the night, and resume wandering the next morning. Wandering in daylight rather than at night probably increases the risk of predation, but has the advantage of allowing the larvae to use visual cues in selecting a spinning site.

Although we have not proved the point, our data suggest that the suitability of a potential cocoon site is determined by the larva's negative phototaxis and positive thigmotaxis. This tends to hide the cocoon. We suggest that the larva is led to the spinning site by positive geotaxis and, sometimes, by its ability to orient to objects visually. An endogenous factor lengthens the wandering phase, decreasing the probability that larvae in trees will spin cocoons before reaching the ground. This is adaptive because a cocoon that is hidden among the leaves of a tree in summer, will probably be exposed to view in winter.

The exposure of the larva to predation as it wanders in search of a spinning site seems to argue against the adaptive value of this behavior if one is not aware that most pupae in cocoons on trees are destroyed by woodpeckers during the winter (Waldbauer & Sternburg, 1967b; Waldbauer et al., 1970). The wandering phase lasts an average of 3.5 hours, but the larva is in the open for only a brief portion of this time. We do not doubt that this relatively brief exposure is more than offset by the advantage of spinning in a site where the cocoon is hidden from view during winter.

SUMMARY

The location of the overwintering cocoons of *Hyalophora cecropia* affects the probability that they will be attacked by vertebrate predators in winter. In this light we examined the selection of the cocoon site by the larvae, and the effect on this behavior of environmental factors in the suburban residential plantings in which cecropia is most common in central Illinois. Feeding larvae are sedentary and do not normally leave the host plants, shrubs and trees of many species. Between 3 and 9 hours ($\bar{x} = 5.7$) after sunrise, mature fifth instars spend a mean of 38 minutes emptying the gut, and then begin to wander. Wandering usually lasts from less than an hour to 8 hours ($\bar{x} = 3.5$), cocoon spinning beginning between 4 and 14 hours ($\bar{x} = 8.7$) after sunrise. On cool days the larvae may rest and resume wandering the next morning. The cocoon site is always selected in daylight. Larvae which feed in shrubs almost always spin close to the ground on the same or a contiguous shrub. Larvae which feed on trees may spin on one of its branches, where the cocoon is exposed to view in winter, or they may migrate to spin near ground level in shoots at the base of the tree or in a nearby shrub where they are likely to be hidden in winter. In suburban plantings between 65% and 71% of the larvae in trees spin near ground level. Larvae locate distant shrubs by their ability to orient to silhouettes from a distance. The larva is exposed to predation as it wanders from a tree, but this is offset by the advantage of spinning the cocoon where it will be hidden from woodpeckers in winter.

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ANTHERAEA POLYPHEMUS (SATURNIIDAE) AND BIBLIS HYPERIA
(NYMPHALIDAE) IN TEXAS

The statement was made (Ferguson 1972, *Moths of North America*, Fasc. 20.2B, E. W. Classey Ltd., London, p. 200) that although *Antheraea polyphemus* (Cramer) is the most widely distributed of North American Saturniidae it has not been reported from counties of the southern coastal bend of Texas. On 18 September 1976, I took eight males of this species in black light traps at the Risken Ranch (27°9'N, 97°41' W) in Kenedy Co., definitely a southern coastal bend county. Three were kept as specimens, and one of the three was deposited in the U.S. National Museum. I had previously reported other, more northerly coastal bend records (Kleberg and San Patricio Co.) to J. F. Gates Clarke and at his suggestion sent voucher specimens to the National Museum.

Biblis hyperia (Cramer) (Nymphalidae) is reported by Howe (1975, *The butterflies of North America*, Doubleday, Garden City, NY, p. 125) to occasionally stray into the Brownsville region of Texas. In the Texas A & I University–Kingsville collection are three specimens (one female, two males) taken by members of my entomology class and myself at the R & B Welder Refuge near Sinton, San Patricio Co., Texas, on 30 November 1973. Some years previous to this date, Carroll Williams of the Corpus Christi (Texas) Museum mentioned to me that he had taken the species at the Welder Refuge. Good evidence exists that there is, or has been, a resident population of this species in the United States. Williams' specimens were taken at the "Hackberry Motte," mine ca. 6 mi distant at the "Bolsa," both areas of dense wood along the Aransas River.

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