

LIGHT-TRAP CATCHES OF MOTHS WITHIN AND ABOVE THE CANOPY OF A NORTHEASTERN FOREST

A. W. THOMAS

Natural Resources Canada, Canadian Forest Service-Fredericton,
Fredericton, New Brunswick E3B 5P7, Canada

ABSTRACT. A catch of 10,991 moths, comprising 311 species in 15 selected families, was identified from two 22-watt blacklight traps operating for 29 nights between 21 June and 30 July 1990. Nightly catches ranged from 4 to 824 individuals per trap. In the within-canopy site, 6,088 individuals of 255 species were identified, whereas in the above-canopy site, 4,903 individuals of 269 species were identified. There were 213 species common to both sites. The coefficient of similarity (of species) between sites was 0.862 (Morisita-Horn index). The percentage complementarity between sites was 31.5 (Marczewski-Steinhaus distance).

Moths in the family Noctuidae dominated the identified catches, accounting for 43.5% of the species and 36.6% of the individuals within the canopy, and 49.4% of the species and 52.4% of the individuals above the canopy. Moths in the family Geometridae were the next most common identified group, forming 33% of individuals in the canopy and 26% of individuals above the canopy. Members of no other single family formed more than 8% of the identified individuals. Several non-tree-feeding species and four known migrants were collected only above the canopy.

Each trap's nightly catch was separated into 30-minute sequential samples, 16/night, between 2130–0530 h ADT. Individuals were trapped all night, but on average catches peaked at 2300–2330 h, two hours after sunset. On nights when a trap's catch exceeded 300 individuals, peak numbers occurred later than on nights when fewer individuals were trapped. When species inventory was summed over the 29 nights, full-night sampling, as opposed to partial-night sampling, was necessary to maximize the number of species. Species accumulation curves were steepest during the last week of June and shallowest during the first two weeks of July. Species richness was estimated as being between 309 and 312 species in the selected families (Chao 1 estimator) during the 29-night sample period.

Additional key words: 30-minute samples, within-night activity, partial-night samples, inventory, species richness.

Light traps are a common tool for elucidating the biology of moth species, and probably are the most widely used insect traps (Southwood 1978, Muirhead-Thomson 1991). They have been used for faunal surveys of both pest and non-pest moth species in the United Kingdom since 1933 (Taylor 1986). Sample et al. (1993) used light traps to evaluate the effect of insecticide spray on non-target Lepidoptera, and recent studies on diversity of moth communities using light traps include Magurran (1985), Robinson and Tuck (1993), Thomas and Thomas (1994).

In faunal surveys, questions arise with regard to sampling effort and detection of species. One such question is whether operating a light trap for only part of a night yields as many species as when a trap is operated throughout the night. Such partial-night sampling is attractive if a collection is being made from a sheet when the lamp is not incorporated into a trap (Profant 1989, Robinson & Tuck 1993), or when

many hundreds of moths are likely to be captured resulting in an inordinate amount of damage to specimens and time for sorting and identification (Sample et al. 1993, Thomas & Thomas 1994). Other questions relate to the total number of species in the area and the effort required to find them (Wolda 1983, Soberon & Llorente 1993, Colwell & Coddington 1994).

The present study was part of an ongoing analysis of the population dynamics of spruce budworm, *Choristoneura fumiferana* (Clemens) (Tortricidae), where light traps were used to detect migration of spruce budworm moths into the study plot. Many other species were trapped along with spruce budworm, and the objectives of this study were to compare, over a 29-night sample period: (1) the between-night light-trap catches of moths at two sites (within and above a forest canopy), based on number of individuals; (2) the average within-night light-trap catches of moths at the two sites, based on number of individuals and number of species captured during sequential 30-minute periods; (3) the similarity and complementarity of the catches at each site, based on numbers of species and individuals; (4) partial-night sampling with full-night sampling for species-inventory purposes; and (5) species accumulation curves between sites, and to estimate local species richness.

METHODS

Beginning on 21 June, and ending on 30 July 1990, two 22-watt black-light traps (Universal Light Trap, Bioquip Products, California) were operated in the Peter Brook study area of the Acadia Forest Experiment Station, near Fredericton, New Brunswick, Canada. For a variety of reasons, full-night trap data from both traps are available for only 29 of the potential 40 nights. A description of the study area is given in Thomas and Thomas (1994).

A within-canopy trap, with the lamp at 6.4 m above the ground, was on a platform, 3×1.5 m, on a tower within the closed crowns of balsam fir trees, *Abies balsamea* (L.) Miller (Pinaceae). The otherwise touching branches were trimmed to leave a clearing of 3×1.5 m. A blue plastic sheet, 1.8×2.4 m, was stretched above the platform at a height of 2.4 m above the lamp. This sheet made direct observation of the lamp impossible from above, although the reflection of the light off the foliage of adjacent trees gave a glow to the immediate area that was obvious from the ground. An above-canopy trap was on a tower with the lamp at about 1 m above the tips of the tallest trees in the immediate vicinity (lamp at 9.5 m above the ground). This trap was on a platform similar to that of the within-canopy trap but had no plastic sheet above it.

The lamp was above the rim of the aluminum collecting funnel in the within-canopy trap, and below it in the above-canopy trap. The

TABLE 1. Total number of identified species trapped by family, and number and percentages of species and moths by site (excludes uncounted numbers of all other families). Geometridae excludes *Eupithecia* spp., and the spruce budworm is the only recorded taxon in Tortricidae.

Family	Within-canopy site						Above-canopy site			
	Total species	Species		Moths			Species		Moths	
		Number	%	Number	%		Number	%	Number	%
Hepialidae	1	1	0.39	3	0.05		1	0.37	1	0.02
Sesiidae	1	1	0.39	11	0.18		1	0.37	27	0.55
Cossidae	1	1	0.39	1	0.02		0	—	—	—
Tortricidae	1	1	0.39	450	7.40		1	0.37	192	3.92
Limacodidae	4	4	1.57	64	1.05		3	1.12	24	0.49
Thyatiridae	2	1	0.39	3	0.05		2	0.74	6	0.12
Drepanidae	3	3	1.18	50	0.82		2	0.74	36	0.73
Geometridae	86	79	31.00	2012	33.00		67	24.90	1273	26.00
Lasiocampidae	3	2	0.78	163	2.68		3	1.12	62	1.26
Saturniidae	4	3	1.18	40	0.66		3	1.12	29	0.59
Sphingidae	10	7	2.75	103	1.69		10	3.72	57	1.16
Notodontidae	27	23	9.02	444	7.29		24	8.92	369	7.53
Arctiidae	18	16	6.27	441	7.24		15	5.58	221	4.51
Lymantriidae	4	2	0.78	76	1.25		4	1.49	36	0.73
Noctuidae	146	111	43.50	2227	36.60		133	49.40	2570	52.40
Totals	311	255		6088			269		4903	

effect of these configurations was that the lamp of the within-canopy trap was potentially visible horizontally (although partially restricted by the fir foliage), but the lamp of the above-canopy trap was visible only from above the forest. The towers were 76 m apart with the base of the above-canopy tower at a slightly higher elevation than the remainder of the study plot. The lamps were switched between traps on alternate nights.

Each trap was equipped with an automatic time-interval collecting device (King et al. 1965, Siddorn & Brown 1971, Smith et al. 1973). Each trap's nightly catch was separated into 16 sequential samples of 30-minute duration. The lamps were switched on at 2130 h and switched off at 0530 h. Sunset and sunrise were at 2120 h and 0536 h on the first trap-night and 2058 h and 0606 h on the last. However, the sky was noticeably lighter at 30 min before sunrise and stayed light for 30 min after sunset.

All individuals in 14 of the 15 selected lepidopteran families listed in Table 1 (see also Appendices I and II) were identified to species and counted, except for *Eupithecia* spp. (Geometridae) which were not included in any totals. For Tortricidae, only spruce budworm moths were identified and counted. Further details of moth identification are given in Thomas and Thomas (1994). Data analysis was based on 311 species, although there were at least two additional species present. *Syngrapha*

alias (Ottolengui) (Noctuidae) and *Syngrapha abstrusa* Eichlin and Cunningham (Noctuidae) had identifications confirmed from male genitalia but many individuals were females that I could not positively identify. Thus, the 54 individuals that were recorded as one species (*S. "alias"*) included both *alias* and *abstrusa*. Klaus Bolte identified 10 individuals of *Hydriomena renunciat*a (Walker) (Geometridae) and 17 individuals of *Hydriomena divisaria* (Walker) (Geometridae). I could not assign a further 126 individuals to either taxon and thus the 153 individuals were listed as one species (*H. "renunciat*a"). It is also possible that the 44 individuals identified as the single species *Xestia dolosa* Franclemont (Noctuidae) could be *Xestia adela* Franclemont (Noctuidae) or a mix of both species. Similarly, the 232 individuals recorded as *Hypagyrtis piniata* (Packard) (Geometridae), could be *Hypagyrtis unipunctata* (Haworth) (Geometridae) or could include both species. I have reared *H. piniata* from larvae collected at the study plot.

No detailed weather data were measured except for a continuous temperature reading at the within-canopy trap. The total numbers of individuals, in the selected families, caught in each trap per night were counted and the actual numbers were used for between-night comparisons. Descriptions of the within-night moth activity were based on geometric means. The numbers of individuals caught during a 30-minute time-period were transformed as $\log(\text{catch}+1)$ and considered as one replicate for that time-period. When these log values were added together and divided by the number of trap-nights ($n=29$), the geometric mean catch for a time-period could be calculated by subtracting 1 from the antilog of the mean log value. These geometric means gave a measure of the abundance of individuals trapped at each time-period and also the distribution of catches during the night. Such an averaging of the catch per time-period over the 29 nights ensured that activity patterns during nights of small catches were not overshadowed by nights with large catches (Williams 1935, 1937, 1939, 1951, 1964, Williams et al. 1955, Hardwick 1972, Bowden & Gibbs 1973, Persson 1976, Douthwaite 1978, Zar 1984). The within-night distribution of species was determined simply by accumulating all the species trapped during each 30-minute period over the 29 nights. The accumulated number of species for each summed 30-minute period was plotted as the percentage of the total number of identified species collected at the site.

The two sites were compared for similarity of species by determining the Morisita-Horn index for coefficient of similarity (Wolda 1981, Magurran 1988), and the complementarity of the two species lists was determined using the Marczewski-Steinhaus distance (Colwell & Codrington 1994). The former index takes into account the relative abundance of the species in each trap while the latter uses the number of

species in common between the two traps and the number of species unique to either trap. A similarity index of unity would be expected from two random samples (each of about 5,000 moths) drawn from the same population (see Wolda 1981, Fig. 4). An index of zero would occur if the traps had no species in common. Complementarity of two species lists varies from zero when the lists are identical, to unity when the lists are totally distinct.

The effect of partial-night sampling on the species inventory was determined in the following manner. It was assumed that sampling would begin at dusk and end before dawn. Species were summed by time-period beginning with the total number of species collected during the 29 replicates of time-period 1. Species collected during all 29 replicates of time-period 2 that were not collected during time-period 1 were considered "new." These "new" species from time-period 2 were summed. Similarly, "new" species collected during all 29 replicates of time-period 3 were summed, followed by "new" species from time-period 4, etc. The results are presented as bar charts of the number of "new" species versus time-period. The "loss" of species caused by any curtailment of collecting before dawn could be readily determined.

The number of species was accumulated chronologically by adding each night's catch, from one trap, to the accumulated catch for that trap. This cumulative number of species was plotted against the sample date to get a species accumulation curve for each site (Colwell & Coddington 1994). An estimate of the potential richness of the sites for the sample period was determined using the Chao 1 estimator. This method involves squaring the number of singletons (i.e., the number of species represented by a single individual), dividing it by twice the number of doubletons and adding this estimate of undetected species to the number of collected species (Colwell & Coddington 1994). This estimator performs especially well when there is a preponderance of relatively rare species (Colwell & Coddington 1994) as is the case with the present data set (Appendices I & II; see also Thomas & Thomas 1994, Table 2).

RESULTS

A total of 10,991 individuals representing 311 species in 15 selected families was identified from the two sites. The 6,088 individuals in the 255 species identified from the within-canopy site have been listed, along with the extreme dates of capture and numbers of specimens, in Thomas and Thomas (1994). A total of 4,903 individuals in 269 species was identified from the above-canopy site and are listed, with extreme dates and numbers, in Appendix I. This list identifies the 213 species that were common to both sites and the 56 species that were unique

to the above-canopy site. Appendix II lists the 42 species that were unique to the within-canopy site.

The breakdown of the selected catches into numbers of species and individuals per family, with these numbers as percentages of totals, for each site is shown in Table 1. Members of the families Noctuidae and Geometridae formed the bulk of the identified catch in each trap. Within the canopy: noctuids accounted for 43.5% of the identified species, and with 36.6% of the identified individuals formed the largest single-family catch; geometrids with 31.0% of the identified species and 33% of the identified individuals formed the second largest single-family catch. Above the canopy: noctuids formed 49.4% of the identified species and accounted for 52.4% of the identified individuals; geometrids with 24.9% of the identified species and 26.0% of the identified individuals were again the second largest single-family. Members of the other 12 selected families (i.e., families other than Tortricidae) were relatively rare at each site, with members of no single family forming more than 8% of the total individuals.

Night vs. size of catch. The total number of individuals captured each night varied between 34 and 1,372 with the three lowest catches occurring on nights having the lowest temperatures (9–11°C) (Table 2). The size of a night's catch at each site was usually similar with the differences in the numbers of individuals trapped between sites being less than three-fold on 24 nights. On the remaining five nights (26/27 June, 5/6 July, 6/7 July, 10/11 July, 17/18 July) the within-canopy catch was greater than four times that of the above-canopy catch (Table 2). Greater variation in catch size was seen in the above-canopy site (ranging from 4 to 824 individuals/night), than in the within-canopy site (30 to 548 individuals/night).

Within-night activity: individuals. The pattern of the within-night catches, based on the geometric mean number of individuals per time-period, was similar at each site. There was a rapid build-up in numbers from low during time-period 1 (2130–2200 h), to high during time-period 4 (2300–2330 h) that was followed by a gradual decrease in numbers until time-period 16 (0500–0530 h) (Fig. 1). When the nightly catches were grouped, based on catch size, the activity patterns differed within and between sites:

i. Within-canopy site. On the seven nights when the catches exceeded 300 individuals per night, numbers peaked late and were maintained for a longer period than on nights when catches were lower (Fig. 2A). This catch pattern was associated with nights when average temperature was 19.4°C at 2400 h. On the eight nights when catches were between 201 and 300 individuals, the catch pattern was similar to that of the high-catch nights, with many individuals flying in the middle of the night

TABLE 2. Numbers of identified moths trapped above and within the canopy on 29 nights. Temperature in degrees Celsius, as recorded at 2400 h.

Day of year	Date	Number of individuals			Temperature
		Above	Within	Total	
172	21/22 June	114	278	392	12
176	25/26	149	260	409	15
177	26/27	71	347	418	18
178	27/28	824	548	1372	16
179	28/29	45	126	171	12
180	29/30	233	264	497	14
183	02/03 July	62	105	167	13
185	04/05	345	313	667	19
186	05/06	8	37	45	9
187	06/07	4	30	34	10
189	08/09	146	125	271	14
190	09/10	60	53	113	17
191	10/11	30	161	191	17
192	11/12	21	37	58	11
193	12/13	75	114	189	13
194	13/14	76	160	236	13
195	14/15	99	279	378	20
196	15/16	462	369	831	21
197	16/17	237	251	488	23
198	17/18	57	327	384	20
199	18/19	294	345	639	22
200	19/20	192	254	446	21
201	20/21	234	278	512	19
202	21/22	50	132	182	16
203	22/23	104	80	184	15
204	23/24	105	100	205	17
205	24/25	411	393	804	20
206	25/26	270	235	505	19
210	29/30	116	87	203	23

(Fig. 2A). The average temperature on these nights was 17.9°C at 2400 h. When a night's catch was between 101 and 200 individuals ($n=8$ nights), there was still a rapid build-up in numbers as seen in the "big-catch" nights but there was a sharp drop in numbers after 2330 h (time-period 4) (Fig. 2A). On these nights, the average temperature was 14.0°C at 2400 h. When the nightly catches were low (<101 individuals/night, $n=7$ nights), catches remained at a constant low level after 2300 h (time-period 3) (Fig. 2A). The temperature averaged 14.6°C at 2400 h.

ii. Above-canopy site. When nightly catches totalled >300 individuals ($n=4$ nights), the mean number of individuals per time-period increased rapidly and remained high from 2230 h to 0300 h (time-periods 3 to 11) (Fig. 2B). The average temperature was 19.0°C at 2400 h. When nightly catches were between 201 and 300 individuals/night ($n=5$ nights), the mean number of individuals per time-period increased slowly and did not reach a plateau until after 2400 h (time-period 6) (Fig.

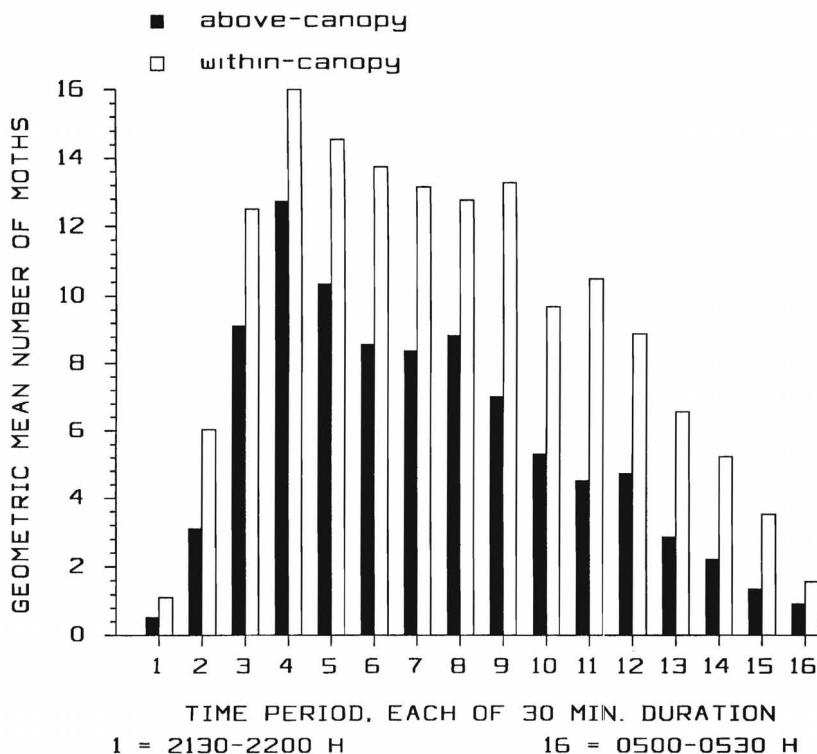


FIG. 1. Average within-night light-trap catch pattern of individuals above and within the canopy. Each bar represents the geometric mean catch of twenty nine 30-minute periods. Sunset and sunrise were at 2120 h and 0536 h on the first trap-night and 2058 h and 0606 h on the last.

2B). The average temperature was 19.4°C at 2400 h. The pattern of the catch of individuals on nights when the catch was between 101 and 200 individuals/night was markedly different from the pattern seen in the within-canopy trap for this grouping of individuals (Fig. 2B). There was no rapid rise in numbers and the mean catch per time-period stayed at a relatively constant low level throughout the night. The average temperature was 16.7°C at 2400 h on these seven nights. On the 13 nights when catches were low (<100 individuals/night) the mean catch per time-period remained constant throughout the night and the temperature averaged 15.0°C at 2400 h.

An examination of the average within-night catch pattern for single species that had sufficient numbers of individuals to detect a pattern, showed that individuals of most species were trapped throughout the eight-hour night. Also, peak catch occurred early in the night, as in e.g.,

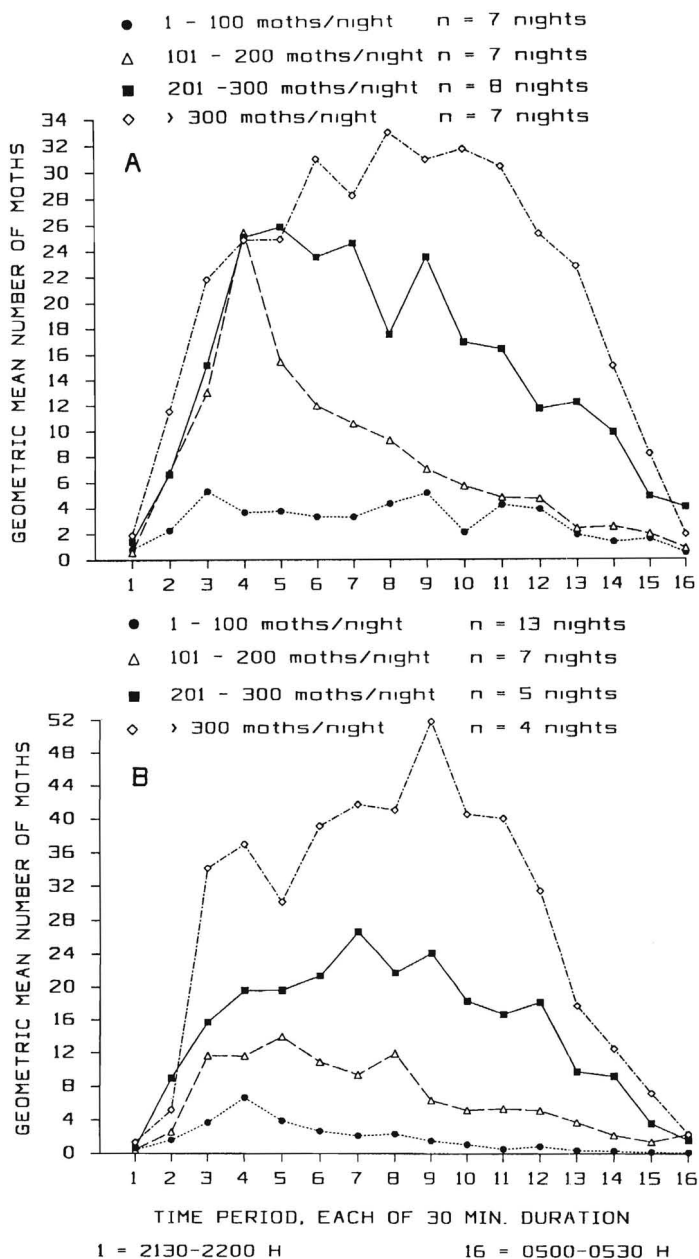


FIG. 2. Average within-night catch patterns of individuals when nights are grouped by size of catch. A: within-canopy site; B: above-canopy site.

TABLE 3. Geometric mean number of individuals trapped per 30-minute period for *Elaphria festivoides* (9681) and *Malacosoma disstria* (7698) in the above-canopy trap (A) and the within-canopy trap (W). All numbers multiplied by 100 to remove decimals. Maxima in bold.

Species	Site	Mean number of individuals/time-period ($\times 100$)															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
9681	A	7	59	112	117	65	35	6	21	16	20	15	4	7	7	0	0
9681	W	7	33	41	72	39	28	33	21	7	26	12	9	7	4	9	7
7698	A	0	8	8	12	8	23	16	33	46	12	18	12	8	12	4	0
7698	W	4	16	16	24	35	23	55	67	87	66	42	29	8	12	6	0

Elaphria festivoides (Gn.) (Noctuidae) whose members were trapped in all time-periods but whose numbers peaked between 2300 and 2330 h (time-period 4) (Table 3). A few species showed peak catches later in the night, e.g., *Malacosoma disstria* Hbn. (Lasiocampidae) at 0130–0200 h (time-period 9) (Table 3), whereas *Acronicta retardata* (Wlk.) (Noctuidae) had peak catches at 0200–0230 h (time-period 10). There was usually no difference in average catch patterns between the two sites for individuals of the same species (Table 3).

Within-night activity: species. The number of species captured during each summed time period is shown as a percentage of the total number of species captured at that site (Fig. 3). For example, 132 species were trapped during the 29 nights between 2330 h and 2400 h (time-period 5) in the within canopy trap. These 132 species represented 51.8% of the total species ($n=255$) taken within the canopy. The percentage of the species captured was similar for both sites. There was a rapid increase in the number of species collected in subsequent summed 30-minute sampling periods, from about 7% of the total species between 2130–2200 h (the summed 29 samples from time-period 1) to about 44% at 2300–2330 h (the summed 29 samples from time-period 4). This proportion stayed at a plateau until 0200–0230 h (time-period 10) and then declined. Thus, a 30-minute collection taken on each of the 29 nights between 2300 h and 0230 h would have resulted in about 44–50% of the total species being collected. After 0230 h the number of species in each summed 30-minute collection began to decline until 0500–0530 h (time-period 16) when only 14% of the species were collected.

Similarity of catches between sites. In general, comparison of single-species catches between sites showed no great differences in numbers of individuals trapped, although more individuals were usually taken at the within-canopy site (Appendix I). Moths identified as *Hyppagyrtis piniata* (Pack.) (Geometridae) were an exception in that they were taken five times more frequently within the canopy (193 vs. 39).

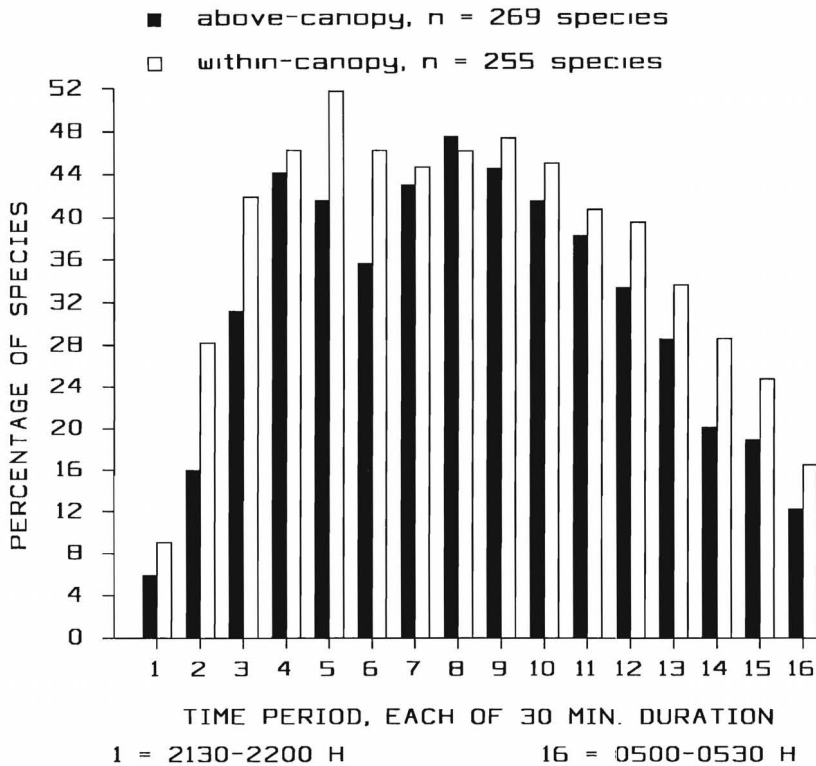


FIG. 3. Average within-night light-trap catches of numbers of species from 464, 30-minute samples per trap between 21/22 June and 29/30 July. Numbers are expressed as percentages of total species trapped at each site.

In contrast, *Callopistria cordata* (Ljungh) (Noctuidae) was 2.7 times more common above the canopy (438 vs. 162). Of the 213 species that were common to both sites, 134 species (63%) were trapped as frequently or more frequently within the canopy (i.e., 50% or more of their members were taken within the canopy). When the 42 species that were unique to the within-canopy site were added, there was a total of 176 species that were more frequent at this site. Of the species common to both sites, 79 (37%) were trapped more frequently above the canopy. Adding the 56 that were unique to this site, each of which was represented by <10 moths, gave a total of 135 species. The five most frequently trapped species of these 56 had larval food plants other than forest trees (Covell 1984): *Sideridis maryx* (Guenee) (Noctuidae) (n=9), food plant unrecorded, but not known to feed on trees (Prentice 1962); *Anticlea multiferata* (Walker) (Geometridae) (n=7), larvae feed on willow-herb; *Caenurgina crassiuscula* (Haworth) (Geometridae) (n=6), lar-

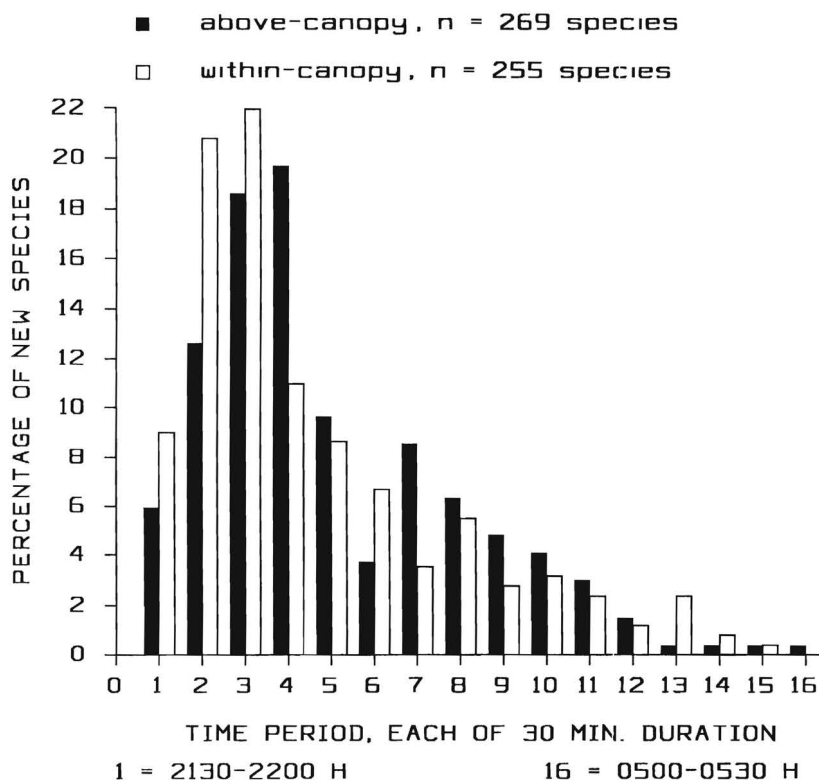


FIG. 4. Average within-night distribution of species new to the inventory based on 464, 30-minute samples per trap between 21/22 June and 29/30 July. Numbers are expressed as percentages of total species trapped at each site.

vae feed on clovers, grasses, lupines; *Apamea lignicolora* (Guenée) (Noctuidae) ($n=6$), larvae feed on grasses; *Apamea amputatrix* (Fitch) ($n=6$), larvae feed on ground plants. In addition, there were four species that are well known migrants (Chapman & Lienk 1981, Covell 1984): *Magusa orbifera* (Wlk.) (Noctuidae) ($n=3$); *Pseudaletia unipuncta* (Haw.) (Noctuidae) ($n=2$); *Agrotis ipsilon* (Hufn.) (Noctuidae) ($n=2$); and *Helicoverpa zea* (Boddie) (Noctuidae) ($n=1$).

Based on the total trap catches from the 29 nights, the Morisita-Horn index for coefficient of similarity between sites was 0.862 and the percentage complementarity between sites was 31.5.

Species inventory and sampling effort. The number of species new to the inventory, expressed as a percentage of total species for each site, is shown plotted over summed time-periods in Fig. 4. For example, 16 species were taken in time-period 1 (2130–2200 h) during the 29

TABLE 4. The number and cumulative percentage of "new" species during the night. Each time-period is based on the sum of 29 nightly samples between 21/22 June and 29/30 July.

Time	Period	"New" species			
		Above-canopy		Within-canopy	
		#	Cum. %	#	Cum. %
2130–2200	1	16	6.0	23	9.0
2200–2230	2	34	18.6	53	29.8
2230–2300	3	50	37.2	56	51.8
2300–2330	4	53	56.9	28	62.8
2330–2400	5	26	66.5	22	71.4
2400–0030	6	10	70.3	17	78.0
0030–0100	7	23	78.8	9	81.6
0100–0130	8	17	85.1	14	87.1
0130–0200	9	13	90.0	7	89.8
0200–0230	10	11	94.1	8	92.9
0230–0300	11	8	97.0	6	95.3
0300–0330	12	4	98.5	3	96.5
0330–0400	13	1	98.9	6	98.8
0400–0430	14	1	99.3	2	99.6
0430–0500	15	1	99.6	1	100.0
0500–0530	16	1	100.0	0	100.0

sample nights in the above-canopy trap. These 16 species represented just 6% of the total number of species ($n=269$) taken in this trap over the entire 29 sample nights. In the second time-period (2200–2230 h), 43 species were taken over the 29-night period in the above-canopy trap, of which 34 (12.6% of the total 269 species) had not been taken during time-period 1. Species new to the inventory increased until 2300–2330 h (time-period 4) and then declined rapidly. For the within-canopy site the number of "new" species increased until 2300 h, 30 min earlier than the above-canopy site, and then fell rapidly (Fig. 4). The cumulative percentage of "new" species for each site (Table 4) shows what effect the curtailment of nightly sampling effort would have had on species inventory. For example, if sampling had ceased at midnight on each of the 29 nights, 33.5% of the species ($n=90$) would not have been collected at the above-canopy site, and 28.6% ($n=73$ species) would have been missed at the within-canopy site. For all species to have been collected, sampling until dawn was necessary on all 29 nights.

Species accumulation curves. The shapes of the curves relating the cumulative number of species collected to the chronological sequence of sample dates were similar for both sites. Species were added rapidly during the last week of June, followed by addition at a much slower rate during the first two weeks of July, and then followed by another rapid increase in species during the last two weeks of July (Fig. 5).

Species richness. The estimated richness of each site for the sample

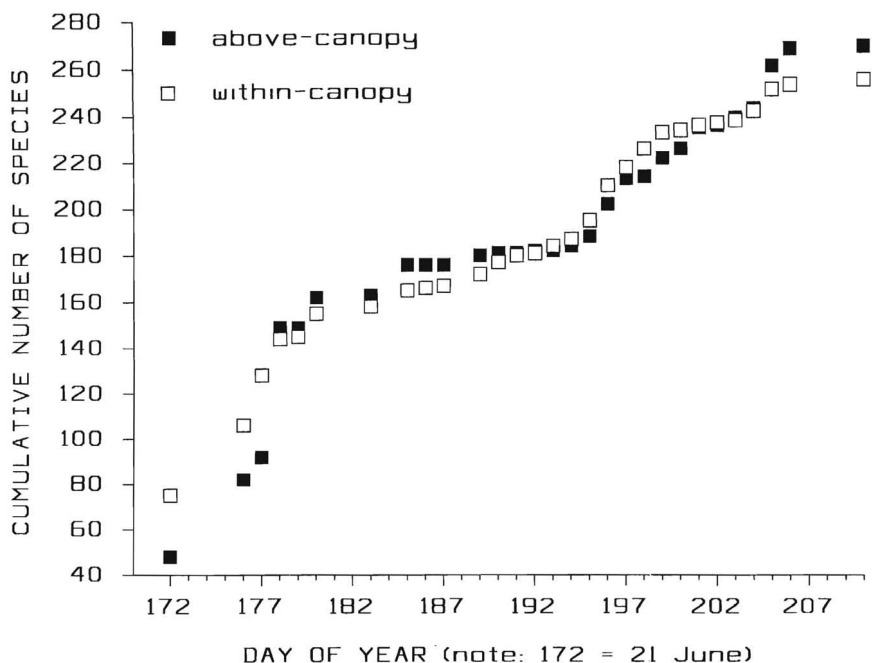


FIG. 5. Species accumulation versus sample date.

period (21 June to 29 July) was determined using the Chao 1 estimator. For the above-canopy site, 51 species were singletons and 30 were doubletons (Appendix I); the estimate of undetected species was thus $2601/60=43$ for an estimated species richness of 312. For the within-canopy site there were 52 singletons and 25 doubletons (Appendices I & II), giving an estimate of 54 undetected species and an estimated species richness of 309. These figures are close to the 311 species trapped during the study period.

DISCUSSION

The differences in catch size between alternate nights was expected. Williams (1937) recorded similar differences for a trap catch involving many species and attributed them to changes in temperature, wind and other weather conditions. In a later study in which two types of trap were compared, it was found that the largest source of variation was the difference in catch size between nights (Williams et al. 1955). Several other studies documented large differences in catches between nights and attributed such differences to weather (wind speed, temperature, rainfall, relative humidity, night-length) moonlight, adult emer-

gence, and moth movement (Bowden 1982, Bowden & Church 1973, Dent & Pawar 1988, Morton et al. 1981, Nemec 1971, Tucker 1983).

In the present study, the factors affecting the size of a night's catch were unknown but weather was undoubtedly important. Apart from the continuous temperature reading at the within-canopy trap, weather conditions and moonlight were not measured. Although high nightly catches (>300 individuals/trap) occurred only above 15°C , low nightly catches (<100 individuals/trap) occurred over the entire temperature range of $9\text{--}23^{\circ}\text{C}$ (Table 2) suggesting that factors other than temperature were also affecting the size of the catch. In a detailed study of the influence of weather and nocturnal illumination on catches of noctuids in Australia, Persson (1976) concluded that night temperature, night wind and nocturnal illumination, in that order, were the most important factors influencing catch. However, 20% of the variance in catch could not be ascribed to local weather or illumination.

The within-night catches of individuals has been determined for several locations with the trapping period varying between 45–130 minutes. The shorter the time period, the greater the accuracy in showing the catch pattern throughout a night. Williams (1935, 1939) operated a trap throughout the year and divided the night into eight periods. This resulted in a catch period of 55 min in mid-summer to one of 110 min in mid-winter. Douthwaite (1978) used a mechanism to segregate the catch into hourly samples, but turned the light off for 15 min between each trapping period of 45 min so that moths attracted during one hour were less likely to be caught in the next. Graham et al. (1964) used 120-min periods during June and July and 130-min periods during August. Stewart et al. (1967), Mitchell et al. (1972), Persson (1976), Morton et al. (1981) and Dent and Pawar (1988) used 60-min periods. All these studies report on the within-night distribution of catches for individual species.

Three papers reported on within-night catches for multi-species data sets. Williams (1939) gave results for 74 moth species collected over a four year period in England. Graham et al. (1964) presented one graph based on 15,111 macrolepidoptera (unknown species number) collected during a three month period in Texas. Persson (1976) gave the hourly distribution, for each of 18 months, of a total catch of 339,000 noctuids in Australia. In each of these three studies, individuals were trapped all night but at different levels which resulted in a period of peak catch. In my study, individuals were also trapped throughout the night; there was a period of peak catch at each site (based on all individuals); and most species had the same catch pattern as the composite multi-species pattern.

Williams (1935) was the first to compare the within-night distribution

of insect catches in light traps on "good" and "poor" nights. He showed "that on the nights which had unusually large captures, the insects seemed to come later in the night, or rather kept up the numbers later, than on poor nights." The highest catches were associated with a high minimum temperature and a flat temperature gradient from dawn to dusk. This thesis was further supported in a later paper (Williams 1939). Persson's (1976) data showed a seasonal change in catch pattern which may be related to the same phenomenon. During the winter, peak catches of male noctuids occurred within three hours of sunset; during the summer it occurred six hours after sunset. In my study, the high-catch nights were associated with high temperatures and the maximum catch occurred later than on nights with small catches.

The observed within-night catch pattern of *Malacosoma disstria* can be compared with the data on this species from Ontario, Canada (Lewis et al. 1993). The catch patterns were very similar—low in the first part of the night with a peak in the middle of the night. However, in Ontario peak catches occurred 3–4 h after sunset, whereas in my study catches peaked in the 30-minute period between 4 h 20 min and 4 h 50 min after sunset (time-period 9) (Table 3). I can offer no explanation for this difference.

The similarity index of 0.862 is lower than expected for two random samples drawn from the same population (see Wolda 1981, Fig. 4). At 31.5%, the complementarity index is also indicative of a difference in species between sites. Several lines of evidence point to there being a migratory component to the above-canopy catch, when compared with the within-canopy catch. These include: the greater number of species, coupled with fewer moths; the slower rate of increase in catch size coupled with the constant size of the catch throughout the night, particularly when nightly catches were in the 101–300 individual range (Fig. 2B); the capture of known migratory species; the greater numbers of *Callopietria cordata* (438 vs. 162), the larvae of which are fern feeders; and the presence of species normally associated with field habitats. The presence of 56 unique species at the above-canopy site is a strong argument for a migratory component at this site.

The all-species-catch pattern (Fig. 3) can be compared with the species accumulation pattern (Fig. 4). Although time-period 8 (0100–0130 h), when summed over the 29 nights, showed the greatest number of species ($n=128$, 47.6% of the total) for the above-canopy site (Fig. 3), only 17 (6.3%) had not been taken before 0100 h (Fig. 4). The data, when summed over 29 nights, show that "new" species were captured throughout the night and that any curtailment of sampling before dawn would have resulted in the "loss" of species. However, the return on investment (in terms of new species captured versus effort when col-

lecting from a sheet, or versus battery-drain when using a battery-operated lamp) diminished rapidly after 2400 h. About 70% of the species were captured during the first 2.5 hours (summed over 29 nights), to catch the remaining 30% required a further 5.5 hours (also summed over 29 nights).

The shapes of the curves relating the cumulative number of species collected to the chronological sequence of sample dates were affected by the typical progression of species in Nearctic latitudes—a flush of species in early summer, a trough in mid-summer, followed by another flush of species in late-summer. No similar quantitative data were found in the literature, but the pattern seen in this study matches the pattern I have seen during 20 years of light-trapping in New Brunswick.

ACKNOWLEDGMENTS

I thank Don Lafontaine and Klaus Bolte, Biological Resources Division, Centre for Land and Biological Resources Research, Ottawa, for the identification of many of the noctuids and geometrids. I appreciate the useful comments on an earlier version of the manuscript from David Wagner, University of Connecticut, and two anonymous referees.

LITERATURE CITED

- BOWDEN, J. 1982. An analysis of factors affecting catches of insects in light traps. *Bull. Entomol. Res.* 72:536–556.
- BOWDEN, J. & B. M. CHURCH. 1973. The influence of moonlight on catches of insects in light traps in Africa. Part II. The effect of moon phase on light trap catches.
- BOWDEN, J. & D. G. GIBBS. 1973. Light trap and suction-trap catches of insects in the northern Gezira, Sudan, in the season of southward movement of the Inter-Tropical Front. *Bull. Entomol. Res.* 62:571–596.
- CHAPMAN, P. J. & S. E. LIENK. 1981. Flight periods of adults of cutworms, armyworms, loopers and others (family Noctuidae) injurious to vegetable and field crops. Search: Agriculture, Number 14. New York State Agric. Expt. Sta., Geneva, New York. 43 pp.
- COVELL, C. V., JR. 1984. A field guide to the moths of eastern North America. Houghton Mifflin, Boston. 496 pp.
- COLWELL, R. K. & J. A. CODDINGTON. 1994. Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. Roy. Soc. Lond. B.* 345:101–118.
- DENT, D. R. & C. S. PAWAR. 1988. The influence of moonlight and weather on catches of *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) in light and pheromone traps. *Bull. Entomol. Res.* 78:365–377.
- DOUTHWAITE, R. J. 1978. Some effects of weather and moonlight on light-trap catches of the army-worm, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae), at Mugu, Kenya. *Bull. Entomol. Res.* 68:533–542.
- GRAHAM, H. M., P. A. GLICK & D. F. MARTIN. 1964. Nocturnal activity of six lepidopterous pests of cotton as indicated by light trap collections. *Ann. Entomol. Soc. Am.* 57:328–332.
- HARDWICK, D. F. 1972. The influence of temperature and moon phase on the activity of noctuid moths. *Can. Entomol.* 104:1767–1770.
- HENDRICKS, D. E. 1985. Portable electronic detector system used with inverted-cone sex pheromone traps to determine periodicity and moth captures. *Environ. Entomol.* 14:199–204.
- KING, E. W., C. D. PLESS & J. K. REED. 1965. An automatic sample-changing device for light trap collecting. *J. Econ. Entomol.* 58:170–172.
- LEWIS, F. P., J. H. FULLARD & S. B. MORRILL. 1993. Auditory influences on the flight

- behaviour of moths in a Nearctic site. II. Flight times, heights, and erraticism. *Can. J. Zool.* 71:1562–1568.
- MAGURRAN, A. E. 1985. The diversity of macrolepidoptera in two contrasting woodland habitats at Banagher, Northern Ireland. *Proc. Roy. Ir. Acad.* 85 B:121–132.
- . 1988. Ecological diversity and its measurement. Princeton Univ. Press, Princeton, New Jersey. 179 pp.
- MITCHELL, E. R., J. C. WEBB, A. H. BAUMHOVER, R. G. ENDRIS, R. W. HINES & S. MASUDA. 1972. Activity of tobacco hornworm moths as determined by electrocutor grid traps baited with a blacklight lamp and virgin females. *Environ. Entomol.* 1:679–682.
- MORTON, R., L. D. TUART & K. D. WARDHAUGH. 1981. The analysis and standardisation of light trap catches of *Heliothis armiger* (Hubner) and *H. punctiger* Wallengren (Lepidoptera: Noctuidae). *Bull. Entomol. Res.* 71:207–225.
- MUIRHEAD-THOMSON, R. C. 1991. Trap responses of flying insects. Academic Press, London. 287 pp.
- NEMEC, S. J. 1971. Effects of lunar phases on light trap collections and populations of bollworm moths. *J. Econ. Entomol.* 64:860–864.
- PERSSON, B. 1976. Influence of weather and nocturnal illumination on the activity and abundance of populations of noctuids (Lepidoptera) in south coastal Queensland. *Bull. Entomol. Res.* 66:33–63.
- PRENTICE, R. M. 1962. Forest Lepidoptera of Canada, Volume 2. Can. Dept. Forestry Bull. 128:77–281.
- PROFANT, D. 1989. The Lepidoptera of a central Florida sand pine scrub community. *J. Res. Lepid.* 28:37–74.
- ROBINSON, G. S. & K. R. TUCK. 1993. Diversity and faunistics of small moths (microlepidoptera) in Bornean rain forest. *Ecol. Entomol.* 18:385–393.
- SAMPLE, B. E., L. BUTLER & R. C. WHITMORE. 1993. Effects of an operational application of Dimilin on non-target insects. *Can. Entomol.* 125:173–179.
- SIDDORN, J. W. & E. S. BROWN. 1971. A Robinson light trap modified for segregating samples at predetermined time intervals, with notes on the effect of moonlight on the periodicity of catches of insects. *J. Appl. Ecol.* 8:69–75.
- SMITH, J. S., J. M. STANLEY & R. N. GUPTON. 1973. Time-interval collecting device for insect traps. USDA ARS-S-20. 5 pp.
- SOBERON, J. M. & J. B. LLORENTE. 1993. The use of species accumulation functions for the prediction of species richness. *Cons. Biol.* 7:480–488.
- SOUTHWOOD, T. R. E. 1978. Ecological methods, 2nd edition. Chapman and Hall, London. 524 pp.
- STEWART, P. A., J. L. LAM, JR. & J. D. HOFFMAN. 1967. Activity of tobacco hornworm and corn earworm moths as determined by traps equipped with blacklight lamps. *J. Econ. Entomol.* 60:1520–1522.
- TAYLOR, L. R. 1986. Synoptic dynamics, migration and the Rothamsted insect survey. 1986. *J. Anim. Ecol.* 55:1–38.
- THOMAS, A. W. & G. M. THOMAS. 1994. Sampling strategies for estimating moth species diversity using a light trap in a northeastern softwood forest. *J. Lepid. Soc.* 48:85–105.
- TUCKER, M. R. 1983. Light-trap catches of African armyworm moths, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae), in relation to wind and rain. *Bull. Entomol. Res.* 73:315–319.
- WILLIAMS, C. B. 1935. The times of activity of certain nocturnal insects, chiefly Lepidoptera, as indicated by a light trap. *Trans. Roy. Entomol. Soc. Lond.* 83:523–557.
- . 1937. The use of logarithms in the interpretation of certain entomological problems. *Ann. Appl. Biol.* 24:404–414.
- . 1939. An analysis of four years captures of insects in a light trap. Part I. General survey; sex proportion; phenology; and time of flight. *Trans. Roy. Entomol. Soc. Lond.* 89:79–131.
- . 1951. Comparing the efficiency of insect traps. *Bull. Entomol. Res.* 42:513–517.
- . 1964. Patterns in the balance of nature. Academic Press, London. 324 pp.

- WILLIAMS, C. B., R. A. FRENCH & M. M. HOSNI. 1955. A second experiment on testing the relative efficiency of insect traps. *Bull. Entomol. Res.* 46:193–204.
- WOLDA, H. 1981. Similarity indices, sample size and diversity. *Oecologia* 50:296–302.
- . 1983. Diversity, diversity indices and tropical cockroaches. *Oecologia* 58:290–298.
- ZAR, J. H. 1984. *Biostatistical analysis*, 2nd edition. Prentice-Hall, New Jersey. 718 pp.

Received for publication 10 October 1994; revised and accepted 29 May 1995.

APPENDIX I. Species list with numbers of moths and extreme dates of capture for the above-canopy site. Species indicated with an asterisk (*) were unique to this site. The numbers in parentheses are the numbers of moths taken at the within-canopy site for comparison. For extreme dates of capture see Thomas & Thomas (1994). Identifications for *Hypagyrtis piniata* (Pack.) are uncertain, and may include or consist entirely of *Hypagyrtis unipunctata* (Haworth); *Hydriomena renunciata* (Wlk.) includes *Hydriomena divisaria* (Walker); *Syngrapha alias* (Ottol.) includes *Syngrapha abstrusa* Eichlin & Cunningham; identifications for *Xestia dolosa* Franclemont are uncertain, and may include or consist entirely of *Xestia adela* Franclemont.

Hepialidae			
<i>Korscheltellus gracilis</i> (Grt.)	25 July	1	(3)
Sesiidae			
<i>Synanthedon acerni</i> (Clam.)	21 June–25 July	27	(11)
Tortricidae			
<i>Choristoneura fumiferana</i> (Clem.)	4–29 July	192	(450)
Limacodidae			
<i>Tortricidia testacea</i> Pack.	25 June–4 July	4	(4)
<i>Tortricidia flexuosa</i> (Grt.)	27 June–25 July	16	(40)
<i>Lithacodes fasciola</i> (H.-S.)	15–25 July	4	(7)
Thyatiridae			
<i>Habrosyne scripta</i> (Gosse)	21 June–18 July	4	(3)
* <i>Pseudothyatira cymatophoroides</i> (Gn.)	16–18 July	2	—
Drepanidae			
<i>Drepana arcuata</i> Wlk.	27 June–23 July	12	(20)
<i>Drepana bilineata</i> (Pack.)	27 June–29 July	24	(25)
Geometridae			
<i>Protitame virginalis</i> (Hulst)	21 June–11 July	5	(9)
<i>Itame pustularia</i> (Gn.)	15–29 July	119	(183)
<i>Semiothisa minorata</i> (Pack.)	27 June–24 July	14	(17)
<i>Semiothisa bicolorata</i> (F.)	8–21 July	6	(4)
<i>Semiothisa bisignata</i> (Wlk.)	15–24 July	8	(8)
<i>Semiothisa sexmaculata</i> (Pack.)	27 June–25 July	9	(5)
<i>Semiothisa signaria dispuncta</i> (Wlk.)	21 June–25 July	469	(724)
<i>Semiothisa pinistrobata</i> Fgn.	25 June–18 July	7	(16)
* <i>Semiothisa oweni</i> (Swett)	4 July	1	—
<i>Semiothisa orillata</i> (Wlk.)	21 June–8 July	5	(3)
<i>Iridopsis larvaria</i> (Gn.)	25 June–18 July	11	(26)
<i>Ectropis crepuscularia</i> (D. & S.)	29 June–25 July	6	(23)

APPENDIX I. Continued.

<i>Protoarmia porcelaria</i> (Gn.)	4-29 July	5	(5)
<i>Melanolophia canadaria</i> (Gn.)	25-27 June	3	(6)
<i>Eufidonia convergaria</i> (Wlk.)	25 June-22 July	6	(12)
<i>Biston betularia cognataria</i> (Gn.)	21 June-24 July	32	(28)
<i>Hypagyrtis piniata</i> (Pack.)	27 June-25 July	39	(193)
<i>Lomographa vestaliata</i> (Gn.)	21 June-15 July	19	(30)
<i>Cabera erythemaria</i> Gn.	27 June-25 July	22	(41)
<i>Cabera variolaria</i> Gn.	21 June-25 July	10	(22)
* <i>Euchlaena serrata</i> (Drury)	20-24 July	2	—
<i>Euchlaena johnsonaria</i> (Fitch)	16-25 July	4	(7)
<i>Euchlaena irraria</i> (B. & McD.)	27 June	2	(4)
<i>Xanthotype urticaria</i> Swett	27 June-4 July	3	(5)
<i>Pero morrisonaria</i> (Hy. Edw.)	25 June-4 July	5	(13)
<i>Nacophora quernaria</i> (J. E. Smith)	25 June-4 July	6	(4)
<i>Campaea perlata</i> (Gn.)	27 June-20 July	5	(12)
<i>Tacparia detersata</i> (Gn.)	21-27 June	5	(8)
<i>Homochlodes fritillaria</i> (Gn.)	21 June-15 July	7	(5)
<i>Metanema inatomaria</i> Gn.	29 June-21 July	3	(11)
<i>Metanema determinata</i> Wlk.	18 July	1	(4)
<i>Metarranthis amyrisaria</i> (Wlk.)	21 June-4 July	4	(3)
<i>Metarranthis hypocharia</i> (H.-S.)	21 June	1	(1)
<i>Probole arnicaria</i> (H.-S.)	25-27 June	5	(15)
* <i>Plagodis kuetzingi</i> (Grt.)	26 June-14 July	4	—
<i>Plagodis phlogosaria</i> (Gn.)	27 June-4 July	5	(7)
<i>Plagodis alcoalaria</i> (Gn.)	26-29 June	2	(4)
<i>Caripeta divisata</i> Wlk.	25 June-29 July	49	(78)
<i>Caripeta piniata</i> (Pack.)	25 June-14 July	5	(9)
<i>Caripeta angustiorata</i> Wlk.	19-29 July	9	(22)
<i>Besma endropiaria</i> (G. & R.)	9 July	1	(6)
<i>Sicya macularia</i> (Harr.)	20-24 July	3	(3)
<i>Eusarca confusaria</i> Hbn.	24 July	1	(1)
<i>Tetracis cachexiata</i> Gn.	21-27 June	12	(39)
<i>Nematocampa resistaria</i> (H.-S.)	20-29 July	9	(39)
<i>Nemoria mimosaria</i> (Gn.)	4-15 July	2	(2)
<i>Cyclophora pendulinaria</i> (Gn.)	21 June-29 July	24	(47)
<i>Scopula limboundata</i> (Haw.)	27 June-24 July	25	(36)
<i>Dysstroma citrata</i> (L.)	4 July	1	(2)
<i>Dysstroma walkerata</i> (Pears.)	27 June-4 July	4	(4)
<i>Dysstroma hersiliata</i> (Gn.)	27 June-19 July	3	(3)
<i>Eulithis explanata</i> (Wlk.)	16-29 July	59	(55)
* <i>Eulithis serrataria</i> (B. & McD.)	24 July	1	—
<i>Hydriomena perfracta</i> Swett	21-29 June	3	(2)
<i>Hydriomena renunciata</i> (Wlk.)	21 June-29 July	74	(79)
<i>Hydria undulata</i> (L.)	29 June-22 July	2	(2)
<i>Spargania magnoliata</i> Gn.	29 June	1	(1)
* <i>Anticlea multiferata</i> (Wlk.)	25 June-10 July	7	—
* <i>Xanthorhoe labradorensis</i> (Pack.)	16 July	1	—
<i>Xanthorhoe abrasaria congregata</i> (Wlk.)	25 June-15 July	3	(8)
<i>Xanthorhoe ferrugata</i> (Cl.)	26 June-20 July	8	(3)
<i>Xanthorhoe lacustrata</i> (Gn.)	26 June-18 July	3	(1)
* <i>Epirrhoe alternata</i> (Muller)	26 June-22 July	2	—
<i>Hydrelia lucata</i> (Gn.)	21 June-19 July	7	(11)
<i>Hydrelia inornata</i> (Hulst)	25 June-20 July	6	(9)
<i>Eubaphe mendica</i> (Wlk.)	16-25 July	2	(4)
<i>Lobophora nivigerata</i> Wlk.	25 June-29 July	86	(63)

APPENDIX I. Continued.

Lasiocampidae			
<i>*Phyllodesma americana</i> (Harr.)	25 June	1	—
<i>Malacosoma disstria</i> Hbn.	8–29 July	59	(136)
<i>Malacosoma americanum</i> (F.)	18–20 July	2	(27)
Saturniidae			
<i>Dryocampa rubicunda</i> (F.)	21 June–25 July	27	(31)
<i>Antheraea polyphemus</i> (Cram.)	27 June	1	(8)
<i>*Hyalophora cecropia</i> (L.)	25 June	1	—
Sphingidae			
<i>Ceratomia undulosa</i> (Wlk.)	21 June	1	(2)
<i>*Sphinx kalmiae</i> J. E. Smith	25 June–29 July	2	—
<i>Sphinx gordius</i> Cram.	21–27 June	4	(9)
<i>Lapara bornbycoides</i> Wlk.	21 June–24 July	15	(18)
<i>Smerinthus jamaicensis</i> (Drury)	8–23 July	5	(14)
<i>Smerinthus cerisyi</i> Kby.	21 June	1	(2)
<i>Paonias excaecatus</i> (J. E. Smith)	27 June–25 July	8	(15)
<i>*Paonias myops</i> (J. E. Smith)	21–27 June	2	—
<i>Pachysphinx modesta</i> (Harr.)	25 June–23 July	17	(43)
<i>*Darapsa photos</i> (Cram.)	27 June–24 July	2	—
Notodontidae			
<i>*Clostera albosigma</i> Fitch	25 July	1	—
<i>Nadata gibbosa</i> (J. E. Smith)	21 June–4 July	7	(16)
<i>Peridea basitriens</i> (Wlk.)	15–25 July	3	(2)
<i>Peridea ferruginea</i> (Pack.)	21 June–29 July	113	(150)
<i>Pheosia rimosa</i> Pack.	27 June–29 July	9	(8)
<i>Odontotia elegans</i> (Stkr.)	18 July	1	(2)
<i>*Notodonta scitipennis</i> Walk.	4–16 July	3	—
<i>Notodonta simplaria</i> Graef	16–25 July	5	(7)
<i>Gluphisia septentrionis</i> Wlk.	21 June–23 July	20	(54)
<i>Furcula cinerea</i> (Wlk.)	25 June–15 July	6	(5)
<i>*Furcula occidentalis</i> (Lint.)	18 July	1	—
<i>Furcula modesta</i> (Hudson)	13–25 July	24	(11)
<i>Symmerista leucitys</i> Franc.	27 June–2 July	3	(2)
<i>*Dasylophia thyatiroides</i> (Wlk.)	27 June–18 July	3	—
<i>Macrurocampa marthesia</i> (Cram.)	29 June–29 July	4	(3)
<i>Heterocampa umbrata</i> Wlk.	21 June–4 July	14	(11)
<i>Heterocampa biundata</i> Wlk.	21 June–11 July	10	(24)
<i>Lochmaeus manteo</i> Doubleday	25 June–25 July	6	(3)
<i>Schizura ipomoeae</i> Doubleday	21 June–25 July	34	(29)
<i>Schizura badia</i> (Pack.)	21 June–21 July	3	(2)
<i>Schizura unicornis</i> (J. E. Smith)	27 June–24 July	7	(10)
<i>Schizura leptinoides</i> (Grt.)	27 June–25 July	17	(8)
<i>Oligocentria semirufescens</i> (Wlk.)	16–23 July	6	(3)
<i>Oligocentria lignicolor</i> (Wlk.)	27 June–29 July	69	(89)
Arctiidae			
<i>Eilema bicolor</i> (Grt.)	15–22 July	6	(22)
<i>Hypoprepia fucosa</i> Hbn.	16–25 July	18	(54)
<i>Holomelina laeta treatii</i> (Glt.)	24 July	1	(31)
<i>Holomelina aurantiaca</i> (Hbn.)	20 July	1	(1)
<i>Holomelina ferruginosa</i> (Wlk.)	20–25 July	2	(7)
<i>Pyrrharctia isabella</i> (J. E. Smith)	15 July	1	(1)
	25 June–2 July	4	(40)

APPENDIX I. Continued.

<i>Spilosoma virginica</i> (F.)	21 June–29 July	33	(39)
<i>Hyphantria cunea</i> (Drury)	21 June–29 July	102	(182)
<i>Apantesis virguncula</i> (W. Kby.)	29 June–24 July	7	(5)
* <i>Apantesis williamsii</i> (Dodge)	15 July	1	—
<i>Halysidota tessellaris</i> (J. E. Smith)	19–25 July	3	(2)
<i>Lophocampa maculata</i> Harr.	21 June–6 July	39	(48)
* <i>Cyrcia oregonensis</i> (Stretch)	21 July	1	—
<i>Ctenucha virginica</i> (Esp.)	27 June–20 July	2	(4)
Lymantriidae			
* <i>Dasychira dorsipennata</i> (B. & McD.)	21 July	1	—
* <i>Dasychira vagans</i> (B. & McD.)	20 July	1	—
<i>Dasychira plagiata</i> (Wlk.)	27 June–29 July	23	(69)
<i>Leucoma salicis</i> (L.)	4–18 July	11	(7)
Noctuidae			
<i>Idia americalis</i> (Gn.)	29 June–29 July	17	(50)
<i>Idia aemula</i> Hbn.	4–25 July	12	(11)
* <i>Idia lubricalis</i> (Gey.)	24 July	1	—
<i>Zanclognatha protumnusalis</i> (Wlk.)	13–16 July	2	(7)
<i>Bomolocha baltimoralis</i> (Gn.)	29 June–25 July	12	(11)
* <i>Bomolocha palparia</i> (Wlk.)	2–19 July	4	—
<i>Pangrapta decoralis</i> Hbn.	26 June–29 July	20	(26)
* <i>Metalectra quadrisignata</i> (Wlk.)	20 July	1	—
<i>Parallelia bistriaris</i> Hbn.	21 June	1	(5)
* <i>Caenurgina crassiuscula</i> (Haw.)	23–25 July	6	—
<i>Catocala sordida</i> Grt.	23–29 July	8	(3)
* <i>Diachrysia aereoides</i> (Grt.)	14–16 July	2	—
* <i>Diachrysia balluca</i> Gey.	24 July	1	—
<i>Chrysanympha formosa</i> (Grt.)	20–25 July	4	(12)
<i>Autographa precatationis</i> (Gn.)	24 July	1	(1)
* <i>Autographa bimaculata</i> (Steph.)	25–29 July	2	—
<i>Autographa mappa</i> (G. & R.)	27 June–24 July	12	(1)
* <i>Autographa ampla</i> (Wlk.)	24–25 July	3	—
<i>Syngrapha altera</i> (Ottol.)	27 June–21 July	6	(4)
<i>Syngrapha octoscripta</i> (Grt.)	24 July	2	(1)
<i>Syngrapha epigaea</i> (Grt.)	17–24 July	2	(2)
<i>Syngrapha viridisigma</i> (Grt.)	19–25 July	3	(2)
<i>Syngrapha alias</i> (Ottol.)	21 June–23 July	32	(22)
<i>Syngrapha cryptica</i> Eichlin & Cunningham	15–19 July	3	(1)
<i>Syngrapha rectangula</i> (W. Kby.)	4–29 July	14	(27)
* <i>Plusia putnamii</i> Glt.	15–16 July	3	—
<i>Plusia venusta</i> Wlk.	15–29 July	3	(2)
<i>Maliattha synochitis</i> (G. & R.)	4 July	3	(1)
<i>Maliattha concinnimaculata</i> (Gn.)	27 June	2	(5)
<i>Pseudeustrotia carneola</i> (Gn.)	25 June–29 July	15	(21)
<i>Leuconycta diphteroides</i> (Gn.)	27 June–18 July	9	(14)
<i>Panthea acronyctoides</i> (Wlk.)	27 June–25 July	24	(47)
<i>Panthea pallescens</i> McD.	26 June–25 July	31	(29)
<i>Charadra deridens</i> (Gn.)	21–28 June	15	(21)
<i>Raphia frater</i> Grt.	21 June–29 July	169	(152)
<i>Acronicta americana</i> (Harr.)	21 June–29 July	38	(18)
<i>Acronicta dactylina</i> Grt.	8–25 July	23	(9)
<i>Acronicta lepusculina</i> Gn.	25 June–19 July	11	(3)

APPENDIX I. Continued.

<i>Acronicta innotata</i> Gn.	27 June–25 July	23	(19)
<i>Acronicta tritona</i> (Hbn.)	27 June–22 July	7	(3)
<i>Acronicta grisea</i> Wlk.	25 June–24 July	18	(18)
<i>Acronicta superans</i> Gn.	27 June–18 July	3	(1)
<i>Acronicta hasta</i> Gn.	26 June–4 July	2	(1)
<i>Acronicta fragilis</i> (Gn.)	27 June–24 July	10	(14)
<i>Acronicta clarescens</i> Gn.	25 June–29 July	181	(162)
<i>Acronicta retardata</i> (Wlk.)	25 June–24 July	84	(49)
<i>Acronicta impleta</i> Wlk.	29 June	1	(1)
<i>Acronicta noctivaga</i> Grt.	16–25 July	2	(2)
<i>Acronicta impressa</i> Wlk.	15–23 July	4	(1)
<i>Acronicta obliterata</i> (J. E. Smith)	27 June	1	(4)
<i>Agriopodes fallax</i> (H.-S.)	26 June–25 July	37	(29)
<i>Harrisimemna trisignata</i> (Wlk.)	14–19 July	4	(4)
<i>Apamea verbascoides</i> (Gn.)	18 July	7	(1)
* <i>Apamea cariosa</i> (Gn.)	22 July	1	—
* <i>Apamea lignicolora</i> (Gn.)	15–25 July	6	—
* <i>Apamea amputatrix</i> (Fitch)	14–29 July	6	—
* <i>Apamea dubitans</i> (Wlk.)	24 July	1	—
* <i>Parastichtis discivaria</i> (Wlk.)	29 July	1	—
<i>Amphipoea velata</i> (Wlk.)	24–25 July	3	(3)
<i>Euplexia benesimilis</i> McD.	21 June–21 July	23	(36)
<i>Phlogophora iris</i> Gn.	27 June–23 July	8	(3)
* <i>Enargia infumata</i> (Grt.)	20–22 July	2	—
* <i>Enargia mephisto</i> Franc.	15 July	1	—
<i>Chytonix palliatricula</i> (Gn.)	25 June–25 July	40	(78)
<i>Dypterygia rozmani</i> Berio	27 June–21 July	3	(1)
<i>Hyppa xylinoides</i> (Gn.)	27 June–29 July	8	(4)
<i>Nedra ramosula</i> (Gn.)	27 June–25 July	3	(1)
<i>Calloptistria mollissima</i> (Gn.)	25 June–25 July	16	(43)
<i>Calloptistria cordata</i> (Ljungh)	25 June–29 July	438	(162)
* <i>Magusa orbifera</i> (Wlk.)	23–24 July	3	—
<i>Proxenus miranda</i> (Grt.)	15 July	1	(1)
* <i>Caradrina morpheus</i> (Hufn.)	18 July	1	—
<i>Elaphria versicolor</i> (Grt.)	21 June–18 July	112	(51)
<i>Elaphria festivoides</i> (Gn.)	25 June–24 July	189	(130)
<i>Apharetra dentata</i> Grt.	15–29 July	26	(24)
* <i>Homohadena infixa dinalda</i> Sm.	24–25 July	3	—
* <i>Cucullia postera</i> Gn.	27 June–24 July	4	—
* <i>Cucullia omissa</i> Dod	26–27 June	2	—
* <i>Sideridis congermana</i> (Morr.)	27 June–2 July	3	—
* <i>Sideridis maryx</i> (Gn.)	21 June–20 July	9	—
<i>Polia imbrifera</i> (Gn.)	4–25 July	14	(6)
<i>Polia purpurissata</i> (Grt.)	24 July	1	(3)
<i>Polia detracta</i> (Wlk.)	27 June–4 July	3	(8)
<i>Polia goodelli</i> (Grt.)	25 June	1	(1)
<i>Polia latex</i> (Gn.)	21–27 June	45	(18)
<i>Melanchra adjuncta</i> (Gn.)	25 June–29 July	41	(25)
* <i>Melanchra pulverulenta</i> (Sm.)	27 June	2	—
<i>Melanchra assimilis</i> (Morr.)	21 June–24 July	26	(12)
* <i>Lacanobia atlantica</i> (Grt.)	24 July	1	—
<i>Lacanobia subjuncta</i> (G. & R.)	29 June–25 July	5	(1)
<i>Spiramater grandis</i> (Gn.)	21–29 June	11	(14)
<i>Spiramater lutra</i> (Gn.)	21 June–29 July	63	(89)
<i>Lacanobia rugosa</i> (Morr.)	27 June–24 July	3	(2)

APPENDIX I. Continued.

<i>*Trichordestra tacoma</i> (Stkr.)	4 July	1	—
<i>Trichodestra legitima</i> (Grt.)	27 June–24 July	21	(10)
<i>*Trichordestra lilacina</i> (Harv.)	18–24 July	3	—
<i>Papestra biren</i> (Goeze)	27 June	1	(1)
<i>Lacinipolia lustralis</i> (Grt.)	29 June–24 July	10	(17)
<i>Lacinipolia anguina</i> (Grt.)	21–27 June	2	(1)
<i>Lacinipolia renigera</i> (Steph.)	18–29 July	3	(1)
<i>Lacinipolia lorea</i> (Gn.)	27 June–25 July	5	(7)
<i>Lacinipolia olivacea</i> (Morr.)	25 July	1	(1)
<i>*Pseudaletia unipuncta</i> (Haw.)	27–29 July	2	—
<i>Leucania multilinea</i> Wlk.	24–25 July	4	(8)
<i>*Leucania commoides</i> Gn.	24 July	1	—
<i>Leucania insueta</i> Gn.	25 June–25 July	9	(24)
<i>Leucania inermis</i> (Fbs.)	27 June–24 July	4	(4)
<i>Leucania pseudargyria</i> Gn.	24 July	1	(1)
<i>Homorthodes furfurata</i> (Grt.)	27 June–29 July	71	(77)
<i>Orthodes crenulata</i> (Butler)	4–29 July	25	(18)
<i>Orthodes cynica</i> Gn.	21 June–29 July	128	(268)
<i>*Agrotis ipsilon</i> (Hufn.)	27 June–2 July	2	—
<i>Euxoa divergens</i> (Wlk.)	11–24 July	3	(2)
<i>*Euxoa tessellata</i> (Harr.)	25 July	1	—
<i>Ochropleura plecta</i> (L.)	26 June–29 July	27	(29)
<i>*Diarsia rubifera</i> (Grt.)	24–29 July	4	—
<i>Diarsia jucunda</i> (Wlk.)	29 June–25 July	19	(23)
<i>*Eurois occulta</i> (L.)	22–25 July	2	—
<i>Eurois astricta</i> Morr.	25–29 July	2	(5)
<i>Xestia dolosa</i> Franc.	14–29 July	34	(10)
<i>Xestia oblata</i> (Morr.)	22–24 July	3	(3)
<i>Xestia elimata</i> (Gn.)	16 July	1	(2)
<i>Xestia badicollis</i> (Grt.)	16–25 July	3	(5)
<i>Aplectoides condita</i> (Gn.)	25 June–19 July	17	(25)
<i>Anaplectoides prasina</i> (D. & S.)	27 June–25 July	15	(8)
<i>Anaplectoides pressus</i> (Grt.)	27 June–24 July	6	(4)
<i>Eueretagrotis perattenta</i> (Grt.)	27 June–24 July	7	(5)
<i>Eueretagrotis attenta</i> (Grt.)	27 June–29 July	71	(60)
<i>Heptagrotis phyllophora</i> (Grt.)	27 June–25 July	20	(39)
<i>Cryptocala acadensis</i> (Bethune)	23–29 July	8	(4)
<i>*Pyrrhia exprimens</i> (Wlk.)	27 June	1	—
<i>*Helicoverpa zea</i> (Boddie)	25 July	1	—
<i>Noctua pronuba</i> L.	24 July	1	(3)

APPENDIX II. List of species unique to the within-canopy site. See Thomas & Thomas (1994) for extreme dates of capture and number of specimens.

Cossidae

Prionoxystus macmurtrei (Guer.)

Limacodidae

Packardia geminata (Pack.)

Drepanidae

Oreta rosea (Wlk.)

Geometridae

Itame brunneata (Thunb.)

Itame anataria (Swett)

Semiothisa aemulataria (Wlk.)

Semiothisa ulsterata (Pears.)

Semiothisa transitaria (Wlk.)

Euchlaena obtusaria (Hbn.)

Euchlaena marginaria (Minot)

Euchlaena tigrinaria (Gn.)

Tacparia atropunctata (Pack.)

Anagoga occiduaria (Wlk.)

Plagodis serinaria H.-S.

Scopula cacuminaria (Morr.)

Ecliptopera silaceata albolineata (Pack.)

Rheumaptera hastata (L.)

Rheumaptera subhastata (Nolcken)

Mesoleuca ruficollata (Gn.)

Perizoma basaliata (Wlk.)

Xanthorhoe iduata (Gn.)

Horisme intestinata (Gn.)

Saturniidae

Anisota virginiensis (Drury)

Notodontidae

Clostera apicalis (Wlk.)

Pelidea angulosa (J. E. Smith)

Heterocampa guttivitta (Wlk.)

Arctiidae

Haploa lecontei (Guer.-Meneville)

Platarctia parthenos (Harr.)

Cycnia tenera Hbn.

Noctuidae

Idia rotundalis (Wlk.)

Zanclognatha pedipilalis (Gn.)

Zanclognatha cruralis (Gn.)

Palthis angulalis (Hbn.)

Lomanaltes eductalis (Wlk.)

Spargaloma sexpunctata Grt.

Syngrapha microgamma nearctica Fgn.

Baileya ophthalmica (Gn.)

Lithacodia muscosula (Gn.)

Apamea cogitata (Sn.)

Oncocnemis riparia Morr.

Polia nimbosea (Gn.)

Xestia youngii (Sm.)
