Population Biology of Orangestriped Oakworm (Lepidoptera: Saturniidae) in Southeastern Virginia[1]

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ABSTRACT Population biology of orangestriped oakworm, *Anisota senatoria* (J. E. Smith), was studied in southeastern Virginia. Egg mass size was larger on *Quercus palustris* Muench., pin oak, compared with *Q. phellos* L., willow oak. Females produced a sex pheromone that attracted male moths. Blacklight traps were not effective for monitoring *A. senatoria* adults. Peak male emergence occurred on 2 July, 4 days earlier than female. The mean life span was 33.5 days in the laboratory. Pupal mortality was high and only 1.2% of the pupae produced moths in 1989 and 1990. Pupae were capable of overwintering for two years in the field. The first report of a second generation from September - November was documented. Second generation *A. senatoria* oviposited more egg masses, infested more trees and had a longer development time compared with first generation. Large egg mass size, pupae that were capable of overwintering for two years and the presence of a second generation may partially explain the consistent *A. senatoria* populations that have occurred in southeastern Virginia.

KEY WORDS Insecta, *Anisota senatoria,* population biology, pheromones, development, pupal mortality, generations.

Numerous reports on the biology of *Anisota senatoria* J. E. Smith (orangestriped oakworm) have been published (Lintner 1889, Lugger 1890, Felt 1905, Houser 1918, Felt 1926, Becker 1938, Beal 1952, Riotte and Peigler 1981, Drooz 1985, Johnson and Lyon 1988). *Anisota senatoria* populations in Connecticut were studied by Hitchcock (1958, 1961a, b, c); however, research has not been conducted on *A. senatoria* populations in Virginia. Data on the biology of *A. senatoria* may provide an explanation for damaging populations which have occurred during the last 8 years in southeastern Virginia (Coffelt and Schultz 1990). Egg mass size, pupal mortality and number of generations varied between Connecticut (Hitchcock 1961b, c) and southeastern Virginia.

Adult *A. senatoria* eclose from overwintering pupae in late June and are present throughout July (Hitchcock 1958). Mated pairs are found on grass blades, low bushes, or tree trunks (Lintner 1889). Yellow eggs are oviposited throughout July on leaf undersides in masses of 200-700 (Hitchcock 1958, 1961b). Eggs are deposited on terminal twigs of lower branches 3-4 m above ground (Lintner 1889). Gregarious green-yellow larvae skeletonize leaves, while

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black fifth instars consume entire leaves except the main vein. Defoliation occurs in late August to September. During September, larvae seek suitable habitats and burrow 7-10 cm in the soil and pupate (Felt 1905). There are one and possibly two generations a year, depending on location (Hitchcock 1958, Drooz 1985).

The objectives of this study were to examine several biological characteristics of *A. senatoria* populations in southeastern Virginia. These characteristics include egg mass size and development, pheromone attraction, adult emergence and trapping, laboratory larval development, pupal mortality, and comparison of first and second generation development, fecundity, and impact.

Materials and Methods

Egg development time and egg mass size. Eggs that were oviposited on *Quercus palustris* Muench., pin oak, and *Q. phellos* L., willow oak, in Norfolk, Virginia Beach, and Chesapeake, VA were used in this study. Freshly oviposited eggs in 1987 and 1989 were examined daily in the field and the number of days to eclosion were determined. The number of eggs per egg mass was counted in the field from 1987-1990.

Pheromone attraction. Baited and unbaited traps were used in 1989 field experiments. Baited traps consisted of virgin females that were collected as they emerged from overwintering pupae. Traps were similar to the design used to capture male California oakworms, *Phryganidia californica* (Packard) (Hochberg and Volney 1984). One virgin female was enclosed in a cylindrical (7 × 15 cm) wire cage suspended above a Pherocon A. M. sticky card (Trece Inc., Salinas, CA). A 5 ml water vial plugged with cotton was included in baited traps. Unbaited traps did not contain a female. Traps (45 baited and 45 unbaited traps) were placed in *Q. phellos* trees in a Norfolk, VA neighborhood, one trap per tree. Traps were 2 m above ground and at least 10 m apart, suspended in trees from 30 June - 5 July, 6 - 11 July, and 12 - 17 July. The number of *A. senatoria* female and male moths captured per trap per day was recorded daily.

Blacklight traps. Three blacklight traps (as described by Gentry et al. 1967) were obtained from the USDA ARS Cotton Research Laboratory, Oxford, NC. Traps were 76 cm in length and contained a single 15 w blacklight bulb. Traps were suspended from *Q. phellos* branches, 2.5 m above the ground, from 21 June - 21 August of both years. Two traps were used in 1987 and one trap in 1988. Traps were placed in Norfolk, VA trees that had a history of *A. senatoria* infestation and were examined daily. The number of female and male moths captured was recorded.

Adult emergence. A Norfolk, VA area that contained *Q. phellos* trees and had a history of large *A. senatoria* populations was selected for this study. Each morning from 8-11 am (EST) 18 June - 9 July, 1990, all female and male moths were counted in the field as they emerged from overwintered pupae. Moth emergence was not recorded on 8 July.

Laboratory development. In July, 1988, *A. senatoria* eggs were pinned on leaf undersides of 15 cm *Q. palustris* cuttings. Upon egg eclosion, five larvae were established per cutting. Cuttings were placed in 100 ml water-filled cups placed in 19 × 11 cm plastic boxes. Boxes were placed in an environmental

chamber maintained at 26.6°C (L) and 21°C (D) and a photoperiod of 16:8 (L:D). Ten replicates were established. Larvae were examined daily and the date that 60% of the larvae molted to the next stage was recorded. Development time for each stage was determined.

Pupal mortality. Fifth instar *A. senatoria* were collected from Norfolk, VA in September of 1988 and 1989 as they crawled to the ground seeking suitable habitats to pupate. Larvae were placed in 41 × 56 cm laboratory boxes with 3 cm of soil and allowed to pupate. Pupae were sexed (Ehrlich et al. 1969) and separated into 16 wooden boxes (33 × 33 cm, 4 cm in depth) in 1988. Eight boxes received female pupae an eight boxes received male pupae, 25 pupae per box. Pupae contained in the boxes were covered with soil. Eight boxes (four with female and four with male pupae) were covered with a wooden lid that had a wire screen mesh. All 16 boxes were buried 5 cm in soil beneath tree canopies on 21 September, 1988. In 1989, pupae were separated into four boxes. Two boxes received female pupae and two boxes received male pupae, 25 pupae per box. Two boxes (one with females and one with males) were covered, and all boxes were buried on 12 October, 1989.

Lids were removed from covered boxes on 14 June, 1988 and 1989 to allow moths to emerge. On 27 June, 1989 eight boxes (four covered and four uncovered boxes) were unearthed and on 27 June, 1990 two boxes (one covered with male pupae, one uncovered with female pupae) were unearthed. Boxes were taken to the laboratory and the pupae were classified as viable, emerged, dead, or parasitized. Viable pupae were unbroken and showed movement when held. Emerged pupae from uncovered boxes had moved to the soil surface and eclosed at the dorsal tip. Dead pupae were broken and hollow. Parasitized pupae attacked by *Lespesia anisotae* (Webber) (Diptera: Tachinidae) were identified by either puparia or characteristic slits in *A. senatoria* pupae. Viable pupae were placed back in the boxes, covered with soil, and all boxes were left uncovered (no wooden lids) and reburied on 27 June, 1989 and 1990. Screened cages were placed over the boxes to capture any emerging moths. Cages were checked daily during July and the number and sex of moths recorded. On 11 October, 1989, and 8 November, 1990, all boxes were unearthed and pupae were classified into the previously described categories. Pupae were dissected to determine viable pupae.

1989 Second generation population studies. Trees in Norfolk were examined for second generation larvae in October, 1989. Second generation *A. senatoria* larval populations were first observed on 25 October, 1989, at the Hampton Roads Agricultural Experiment Station (HRAES), Virginia Beach, VA. The number of larvae and the number of infested trees were counted. Fifth instars were collected (681 larvae) from the HRAES on 1 November, 1989 and placed in 41 × 56 cm plastic boxes field with 3 cm of soil. Boxes were buried 5 cm deep in the field with a screened cage above the box to prevent larval escape. Pupae overwintered in the field boxes and on 18 June, 1990, viable pupae (45) were removed from the boxes, sexed and counted. Viable pupae were separated by sex into 18 × 14 cm plastic boxes with 3 cm of soil and buried under the canopy of a 1.5 m *Q. palustris* tree. A meshed 2.4 × 1.8 m tent was placed over the tree and soil that contained the boxes to capture emerging adults. Pupae were examined daily for adult emergence from 19 June - 10 August, 1990.

On 10 August, pupae were removed from boxes and classified as previously described. An additional category included moths that did not eclose. The 45 viable pupae (23 female and 22 male) were placed in laboratory containers, dissected in September, and categorized.

1990 Second generation population studies. Fecundity of second generation moths was determined in 1990 from 126 *Quercus* located in a completely randomized design (CRD) plot (Coffelt 1992) at the HRAES. The number of egg masses and eggs per mass per *Quercus* species were counted in early October, 1990. Trees infested with second generation larvae in 1990 were also counted. Additional smaller plots of *Quercus* had been planted at the HRAES. There were 181 *Quercus* in these smaller plots and infested trees were counted. Development time of *A. senatoria* was determined on six of the 11 *Quercus* species in the CRD plot. Larvae were examined daily; the date of 60% larval molting to the next instar and the number of live larvae were recorded. Development time and survival in each instar were determined. Percent survival was based on the number of live larvae entering each stage.

Daily air and soil temperatures and rainfall was determined from a weather station located at the HRAES and from a NOAA weather station at the Norfolk International Airport.

Data were subjected to analysis of variance (ANOVA) and differences between three or more means were separated by Student-Newman-Keuls (SNK) test (SAS Institute, 1985). Arcsin transformations were performed on percent survival data to maintain homogeneity of variance (Steel and Torrie 1980).

Results and Discussion

Egg development time and egg mass size. Egg development time was 10.3 ± 0.1 d (range 7.0 - 13.0 d, n = 123). Differences in development time were nonsignificant between 1987 and 1989 ($F = 0.83$, df = 1, 122, $P > 0.05$) and between *Q. palustris* and *Q. phellos* ($F = 2.30$, df = 1, 122, $P > 0.05$). Air temperature during June - July egg development for 1987 and 1989 was similar for Virginia Beach (25.6 and 24.9°C) and Norfolk (26.2 and 24.6°C). Rainfall was similar except in Virginia Beach in 1987 (5.8 cm) and 1989 (14.4 cm). The 1989 wet season did not significantly influence egg development compared to 1987. Egg development in this study was within the range of other reports. Lintner (1889) reported eggs eclosed in 7-10 days in New York. Hitchcock (1961a) observed in Connecticut that eggs took 12 days to eclose. Significantly ($F = 56.74$, df = 1, 213, $P < 0.05$) more eggs per egg mass were found on *Q. palustris* compared to *Q. phellos* (Table 1). These *Quercus* species were frequently defoliated in southeastern Virginia. Egg masses on *Q. palustris* had a mean of 493.5 ± 15.1 eggs (range 147-811). Egg mass size was large in this study, compared with some regions of the country. Hitchcock (1961b) did not report the host in Connecticut but found a mean of 127.2 eggs (range 94-216). In another report, Hitchcock (1958) stated the number of eggs ranged from 200-700. Lugger (1890) reported *A. senatoria* eggs in Minnesota ranged from 350-675. Lintner (1889) reported an average egg mass size of 500 in New York. Hitchcock (1961b) suggested new *A. senatoria* infestations had more eggs per

Table 1. Mean number of *A. senatoria* eggs per egg mass on *Q. palustris* and *Q. phellos*, 1987-1990.

Quercus sp.	Mean ± SEM No. Eggs per egg mass	N*	Range
Q. palustris	493.5 ± 15.1 a†	79	147.0 - 811.0
Q. phellos	370.2 ± 9.0 b	135	112.0 - 616.0

* Number of egg masses sampled 1987 - 1990, Norfolk, VA.
† Means within columns followed by the same letter are not significantly ($P = 0.05$) different (t test, SAS Institute, 1985).

egg mass and declining populations had the least. Results from this study did not support that observation. Low or declining populations were observed in 1987 and higher populations in 1989. However, differences in egg mass size were nonsignificant ($F = 0.44$, df = 3, 213, $P > 0.05$) between 1987-1990. This consistently large egg mass size contributed to large *A. senatoria* populations in southeastern Virginia.

Pheromone attraction. Significantly ($F = 28.64$, df = 1, 89, $P < 0.05$) more males were captured in baited traps compared with unbaited traps (Table 2). A total of 692 males was captured with 98.7% in baited traps. No females were captured on sticky cards and the mean longevity of baited females was 3.7 ± 0.1 d (n = 90). Significantly ($F = 4.11$, df = 2, 44, $P < 0.05$, followed by SNK test) more males were captured on baited traps 6-11 July compared to the other two dates, which indicated peak activity. These data demonstrated that virgin female *A. senatoria* moths produced a sex pheromone that attracted males. Solomon (1973) showed female *A. virginiensis* (Drury), pinkstriped oakworm, produced a sex pheromone and Riotte and Peigler (1981) reported *Anisota* species emitted pheromone and suggested pheromones may be chemically similar for all species. Identification and synthesis of *A. senatoria* sex pheromone could be an effective monitoring tool.

Table 2. Mean numbers of *A. senatoria* male moths captured at traps baited with virgin females, 1989.

	Mean ± SEM No. males captured					
Trap	30 June - 5 July	N*	6-11 July	N	12-17 July	N
Baited	7.8 ± 2.3 a†	14	24.6 ± 6.0 a	18	10.1 ± 3.7 a	13
Unbaited	0.1 ± 0.1 b	14	0.3 ± 0.2 b	18	0.1 ± 0.1 b	13

* Number of traps.
† Means within columns followed by the same letter are not significantly ($P = 0.05$) different (t test, SAS Institute, 1985).

Blacklight traps. The number of females, males, and total moths caught in blacklight traps were not significantly different between years (1987 and 1989, total moths $F = 3.57$, df = 1, 68, $P > 0.05$), dates ($F = 1.29$, df = 22, 68, $P > 0.05$) and traps (1987, F = 2.59, df = 1, 45, P > 0.05). Only 32 female and six male moths were trapped in 1987, and four females in 1988. Moths were not observed at artificial lights during this four year study. One report stated *A. senatoria* moths were attracted to artificial lights (Johnson and Lyon 1988). Riotte and Peigler (1981) reported some *Anisota* species were attracted to lights but species with diurnal males were rarely trapped. Covell (1984) reported *A. senatoria* moths were diurnal and not easily collected. Peigler and Williams (1984) reported male *A. senatoria* moths seek females from approximately 1130-1530 hrs. Blacklight traps are not an accurate monitoring tool for *A. senatoria* populations and pheromone traps or larval counts were more accurate. Riotte and Peigler (1981) reported *A. peigleri* (Riotte) larvae were abundant in northwestern South Carolina but adults were only occasionally attracted to lights because males were diurnal, a situation similar to that observed with *A. senatoria.*

Adult emergence. Daily emergence of female and male *A. senatoria* moths on 20 sample dates in 1990 showed peak emergence occurred on 6 July (Figure 1). The first moth was found on 19 June, 1990, compared with 23 June and 26 June in 1988 and 1989. Mean soil temperatures from September - June for these three years indicated that the earliest emergence date corresponded to higher soil temperatures (September 1987 - June 1988 12.4°C, September 1988 - June 1989 12.2°C, September 1989 - June 1990 12.8°C). Peak female emergence occurred on 6 July and peak male emergence occurred on 2 July (Figure 1), but large numbers of males also emerged on 5 July. The mean number of moths that emerged per day from 18 June - 9 July was 39.8 ± 9.0 females and 18.0 ± 4.3 males. A total of 796 moths were counted; 69% were females and 31% males. Egg monitoring should commence by the first week of July for IPM programs.

Laboratory development. Mean development time (d) for first-fifth instars and the prepupal stage was 7.4 ± 0.2, 6.3 ± 0.1, 5.5 ± 0.1, 5.2 ± 0.1, 5.4 ± 0.2, and 3.7 ± 0.1, respectively. *Anisota senatoria* larvae had a mean developmental period of 33.5 d under conditions of 26.6°C (L) and 2.10°C (D) and a photoperiod of 16:8 (L:D).

Pupal mortality. The significant treatment (covered or uncovered boxes) and year effects (1988 and 1989) are shown in Table 3. Pupal viability was determined on 27 June, 1989 and 1990, after pupae overwintered for nine months (Table 3). Only 1.2 ± 0.6% (n = 500) of the pupae produced adults in July, 1989 and 1990. Therefore, viable pupae that did not emerge in July 1989 and 1990, attempted to overwinter for two years or attempted to emerge in September as second generation adults.

There was a significant treatment effect ($P < 0.05$) due to covered or uncovered boxes (Table 3). Half of the boxes were covered from fall, 1988 and 1988, to June, 1989 and 1990, to prevent predation by small mammals. Hitchcock (1961c) found mammalian predation on *A. senatoria* pupae was a significant source of mortality. A higher percentage of pupae was viable and attempted to overwinter in uncovered boxes compared with covered boxes (Table 3). Covered boxes may have affected pupal survival because of increased soil temperatures and relative humidity in the boxes which provided a better environment for disease. Diseases

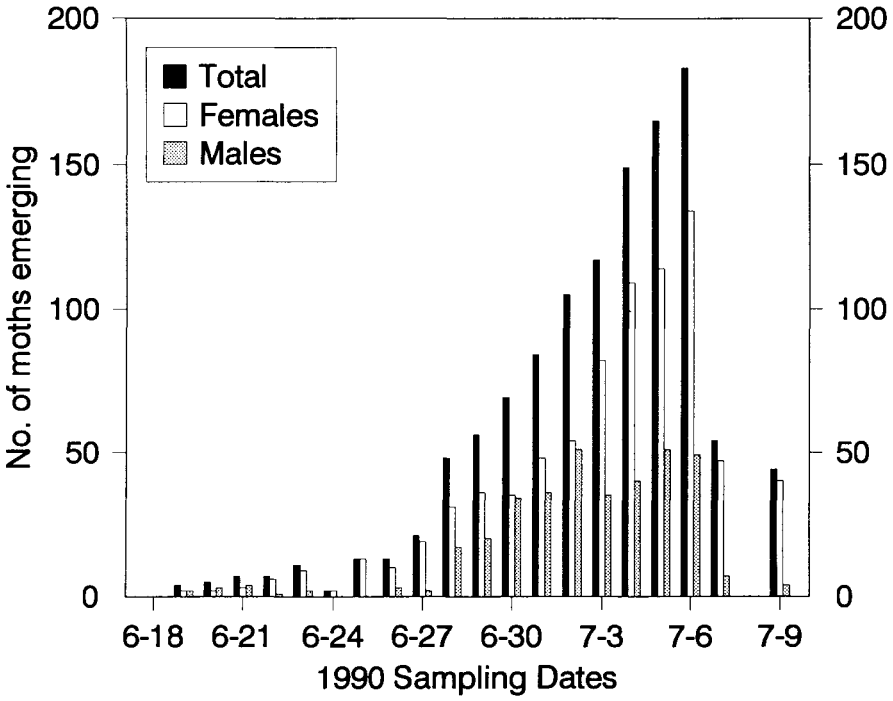

Fig. 1. Daily emergence of female and male *A. senatoria* moths, 1990.

may have contributed to mortality within boxes, although pupae were not examined for diseases in this study. Hitchcock (1961c) found a fungus and cytoplasmic polyhedral virus killed 14.2% of *A. senatoria* pupae.

Pupae were unearthed in fall, 1989 and 1990. Mortality attributed to natural factors, such as predation, diseases, weather, and *L. anisotae* parasitism was not significantly different between covered and uncovered boxes ($P > 0.05$). Covered boxes did not significantly reduce predation, probably because all covered boxes were uncovered from June to October and predation may have occurred. Parasitism rates were similar in covered and uncovered boxes because *L. anisotae* parasitized *A. senatoria* as larvae and emerged from pupae in the spring and early summer.

The percentage of pupae that died from natural mortality factors was significantly ($P < 0.05$) higher in 1989, although parasitism rates were higher in 1988 ($P < 0.05$) (Table 3). Mean soil temperatures and rainfall were similar for overwintering periods from September 1988 - June 1989 (12.2°C and 10.3 cm) and from September 1989 - June 1990 (12.8°C and 12.0 cm). Therefore, additional mortality factors, such as predation and disease, may have influenced these results. All of the pupae that attempted to overwinter for two years or emerge as second generation adults were dead by fall, 1990. Hitchcock (1961c) found 24.1 and 44.8% of *A. senatoria* pupae produced moths in 1959 and

Table 3. Mortality factors of A. senatoria pupae, 1988 - 1989.

	Mean ± SEM percent			
Treatment	PV*	N†	OW	N
Uncovered	59.2 ± 3.4 a‡	5	58.4 ± 3.7 b	5
Covered	39.2 ± 5.0 b	5	36.0 ± 4.1 a	5
Year buried	PD	N	PP	N
1988	79.5 ± 3.0 b	16	19.7 ± 2.8 a	16
1989	95.0 ± 3.7 a	4	2.0 ± 1.1 b	4

* PV = viable pupae on 27 June, 1989 and 1990; OW = pupae that attempted to overwinter for two years or attempted to emerge as second generation adults; PD = dead pupae from natural mortality factors; PP = pupae parasitized by *Lespesia anisotae.*

† Number of boxes.

‡ Means within columns followed by the same letter are not significantly (P = 0.05) different (t test, SAS Institute, 1985).

1960, based on spring and fall pupal counts in soil. In this study, 0.7 and 3.0% of the pupae produced moths, which may be normal for *A. senatoria* populations in southeastern Virginia. Comparisons between data collected by Hitchcock (1961c) and the present study were difficult because of differences in experimental technique, weather conditions, and geographical location.

Lugger (1890) reported that *A. senatoria* pupae remained in laboratory breeding cages for two years. Data in this study showed *A. senatoria* pupae were capable of overwintering for two years in the field. All pupae that were examined in this study (500 pupae) were dead in two years. This small sample size did not show adults emerged after two years, but if larger samples were taken, adult emergence might have been observed.

1989 Second generation population studies. Hitchcock (1958) reported one *A. senatoria* generation in Connecticut. Beal (1952) found one generation in North Carolina but suggested that two may occur. Covell (1984) reported that probably two generations of *A. senatoria* occurred in the southern United States from May to September. The presence of second generation *A. senatoria* from September to November, 1989 and 1990, is first reported in this study. Second generations were only found in populations located at the HRAES. Tree surveys indicated that second generation larvae were not present in Norfolk, VA. Lower pesticide pressure at the HRAES compared with Norfolk may have allowed a second generation to occur.

A total of 20 *Quercus* (9.2%) at the HRAES were infested by second generation populations in 1989. Thirteen *Q. phellos*, three *Q. acutissima*, two *Q. palustris,* and one *Q. rubra borealis* and *Q. falcata* were infested. A higher percentage (51.7%) of first generation larvae in 1988 pupated successfully compared with 1989 second generation larvae (30.4%). Second generation

larvae formed pupae in mid to late November and higher mortality may be due to colder weather.

When 1989 second generation pupae were buried on 19 June, 1990, seven females (6.4%) and one male (1.0%) emerged from 29 June - 7 July, 1990. More adults might have emerged but heavy rain flooded the pupal boxes on 11 -12 July. By 10 August, 1990, 54.5 and 71.0% of female and male pupae were dead, 16.4 and 19.4% were viable, and 22.7 and 8.6% had adults that did not eclose. A subsample (N = 45) of pupae revealed that only one female pupa was viable one year after pupation.

1990 Second generation population studies. Second generation moths were first observed at the HRAES on 28 August, 1990 and by 30 August, 17 female and two males were found on grass blades. Two egg masses were observed being oviposited in mid-September, 1990. The egg stage was 17.0 d for both egg masses, longer than the 10.3 d for the first generation. Mean air temperature and rainfall for September 1990 (20.5°C and 2.6 cm) was lower than June 1990 (22.5°C and 10.0 cm, respectively). Significantly ($F = 9.47$, df = 1, 251, $P < 0.05$) more egg masses were oviposited by second generation females compared with first generation. A mean of 0.7 ± 0.1 and 0.3 ± 0.06 egg masses per tree were oviposited by second and first generation adults. The mean number of eggs per egg mass was not significantly ($F = 1.8$, df = 1, 251, $P > 0.05$) different between generations.

There was significant differences between *Quercus* species in the number of egg masses ($F = 4.48$, df = 10, 125, $P < 0.05$) and eggs per mass ($F = 9.47$, df = 10, 125, $P < 0.05$) (Table 4). These data suggest that *Q. coccinea, Q. bicolor,* Q. *falcata,* and *Q. acutissima* were the most preferred by 1990 second generation *A. senatoria* females. All four of these species held their leaves longer than the other species and green foliage was available until November. *Quercus coccinea* and *Q. acutissima* were among species most preferred by first generation *A. senatoria* populations and *Q. bicolor* and *Q. falcata* were intermediate in preference (Coffelt 1992). *Quercus alba* was the least preferred by both first (Coffelt 1992) and second generation populations.

Infested trees in the CRD plot and HRAES were compared from 1990 first and second generations (Table 5). Although eggs were oviposited on certain *Quercus* species, infestation may differ because fifth instars migrated to other species as trees were 100% defoliated. The 1990 second generation infested more trees than the first generation. Second generation larvae infested 32.5% of all trees available in the CRD plot while first generation infested 23.8%. There were 307 *Quercus* trees available to second generation larvae at the HRAES and 26% were infested. The highest infestations of trees in the CRD plot and at the HRAES occurred on *Q. coccinea* and *Q. acutissima.* These data indicated that oviposition (Table 4) and infestation (Table 5) among *Quercus* species were similar.

Field development and survival by instar of second generation larvae were not significantly different among *Quercus* species so data were pooled (Development and survival, first instar: $F = 2.00$, df = 5, 14, $P > 0.05$; $F = 0.97$, df = 5, 15, $P > 0.05$. second: $F = 0.38$, df = 5, 15, $P > 0.05$; $F = 2.74$, df = 5, 12, $P > 0.05$. third: $F = 1.18$, df = 3, 11, $P > 0.05$, $F = 2.86$, df = 4, 11, $P > 0.05$. fourth: $F = 1.70$, df = 4, 10, $P > 0.05$; $F = 1.29$, df = 5, 13, $P > 0.05$. fifth: $F = 1.29$, df = 4, 7, $P > 0.05$; $F = 0.36$, df = 5, 10, $P > 0.05$) (Table 6). Mean development was

Table 4. Oviposition by 1990 second generation *A. senatoria* on *Quercus* species.

Quercus sp.	Mean ± SEM No. egg masses	N†	eggs per mass	N
Q. falcata	1.9 ± 0.9 a‡	7	111.8 ± 53.6 bc	7
Q. coccinea	1.7 ± 0.3 ab	11	273.9 ± 18.1 a	11
Q. bicolor	1.7 ± 0.5 ab	14	164.0 ± 35.2 b	14
Q. acutissima	1.5 ± 0.4 abc	10	280.1 ± 52.7 a	10
Q. palustris	0.8 ± 0.5 abc	12	55.6 ± 31.0 bc	12
Q. rubra borealis	0.3 ± 0.1 bc	16	50.8 ± 28.6 bc	16
Q. macrocarpa	0.3 ± 0.2 bc	14	38.4 ± 26.6 bc	14
Q. prinus	0.1 ± 0.1 c	12	49.1 ± 37.8 bc	12
Q. nigra	0.1 ± 0.1 c	8	36.0 ± 36.0 c	8
Q. phellos	0.0 ± 0.0 c	9	0.0 ± 0.0 c	9
Q. alba	0.0 ± 0.0 c	13	0.0 ± 0.0 c	13

* Number of tree replicates.
† Means within columns followed by the same letter are not significantly ($P = 0.05$) different Student-Newman-Keuls test (SAS Institute, 1985).

Table 5. Percent of *Quercus* species infested with 1990 first and second generation *A. senatoria* populations.

Quercus sp.	Percent of trees infested: CRD plot first gen.	CRD plot second gen.	HRAES second gen.
Q. palustris	41.7	25.0	20.5
Q. bicolor	35.7	64.3	54.2
Q. acutissima	40.0	80.0	92.0
Q. rubra‡	37.5	12.5	15.0
Q. falcata	28.6	42.8	50.0
Q. coccinea	18.2	100.0	100.0
Q. prinus	8.3	16.7	14.3
Q. macrocarpa	21.4	14.3	14.3
Q. phellos	22.2	0.0	10.7
Q. nigra	0.0	12.5	12.5
Q. alba	0.0	0.0	0.0
Total	23.8	32.5	26.0

‡ *Q. rubra borealis.*

Table 6. Mean development and survival of *A. senatoria* reared on *Quercus* for 1990 second generation larvae.

	Mean ± SEM			
Instar	Days in each instar	N*	Percent survival in each instar	N
First	11.6 ± 0.5	15	67.7 ± 5.4	16
Second	8.4 ± 0.5	16	70.0 ± 6.5	13
Third	7.9 ± 0.5	12	53.0 ± 8.8	12
Fourth	8.3 ± 0.7	11	46.2 ± 7.6	14
Fifth	7.1 ± 0.4	8	54.2 ± 5.4	11

* Number of tree replicates.

longest for the first instar and shortest for the fifth instar. Field development from first to fifth instar for second generation populations was determined in 1990 and compared with first generation populations was determined in 1990 and compared with first generation data (Coffelt 1992). Field development was longer for the second generation (43.3 d, Table 6) compared with the first generation (34.5 d, Coffelt 1992). Colder temperatures and lower rainfall from September - November 1990 (16.6°C and 5.7 cm) compared with June - August 1990 (24.2°C and 16.9 cm) extended the developmental period for second generation larvae. Differences in foliage texture may have lengthened the developmental period for each instar. Additional factors include differences in plant nutrients, parasite and predator activity, and feeding efficiency. Feeny (1970) found high concentrations of water and nitrogen in spring oak foliage that sustained greater herbivore diversity than low nutrient and higher tannin concentrations in late season foliage.

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