tolerance is dose-related rather than time-related. The increase in disappearance rate during periods of chronic intake is partially reversed during subsequent periods of abstinence. Of the five surviving animals, four had decreased rates of disappearance of ethanol after periods in which no ethanol was administered. Metabolic tolerance has also been described in man during, and immediately following, chronic ethanol ingestion (7, 13); however, no significant differences in disappearance rates were found between alcoholics and nonalcoholics when both groups had abstained from ethanol for at least 3 weeks (14). Our observation of partial reversibility of metabolic tolerance in chimpanzees is consistent with those findings.

We have also obtained liver biopsy specimens from each of the chimpanzees both before and after the periods of ethanol administration (15). Histologic and ultrastructural examination indicated marked fatty infiltration after chronic ethanol ingestion. Normal hepatocytes were again predominant, however, in biopsies taken after periods of abstinence, an indication that the fatty changes are reversible. Electron microscopy of hepatic tissue revealed increased amounts of smooth endoplasmic reticulum, large fat droplets, and equivocal enlargement of the mitochondria. These changes in chimpanzee liver tissue are consistent with those observed in man after ethanol ingestion (16).

The development of alcoholism in humans is probably associated with biological and biochemical processses, as well as with social and behavioral factors. Systematic and controlled experimentation with animal models may elucidate the mechanisms underlying the development of this disease process. The observed similarities between the response of the chimpanzee and that of man to ethanol intake suggest that the chimpanzee may be useful in investigating the etiology of alcoholism.

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## Mating Behavior and Life Habits of the Sweet-Bay Silk Moth (Callosamia carolina)

Abstract. The mating activity of the sweet-bay silk moth (Callosamia carolina) was confined to the midday period between 10 a.m. and 3 p.m. The closely related tulip-tree silk moth (Callosamia angulifera), with which Callosamia carolina is often confused, is entirely nocturnal. Reproductive isolation between these sibling species is most probably geared to these differences in circadian activity. Larvae of Callosamia carolina thrived only on the leaves of Magnolia virginiana, upon which the species was double-brooded annually.

The silk moths of the family Saturniidae have fascinated people by their beautiful color patterns, large size, general nocturnal activity, and habit of spinning cocoons composed of silk. The reproductive biology of three silk moths in the genus Callosamia has up to now been unclear. The best known of these three is the promethea moth (C. promethea Drury), which is broadly distributed over the eastern half of the United States. The other two are the tulip-tree silk moth (C. angulifera Walker) and the sweet-bay silk moth (C. carolina Jones) whose ranges primarily encompass the South Atlantic and Gulf Coast states. The adult coloration of all three species is remarkably similar, and males and females of each species exhibit a strong sexual dimorphism. Males differ in color from the female and are darker.

Jones (1) published the first descriptive note on the sweet-bay, or Carolina, silk moth in 1908, where he described the species as a "variety" of the tuliptree silk moth (Callosamia angulifera). Because of similarities in wing coloration and scale patterns, the sweet-bay silk moth was confused with or lumped with the better known tulip-tree silk moth (C. angulifera). Kimball (2), in 1965, pointed out some of the morphological features that separate the two species. However, no one has yet reported any features of the life history of C. carolina that would set it apart as a species distinct from C. angulifera. I conducted a study of C. carolina in Florida over an 18-month period in 1970-71 to clarify its relation to the other two species.

A field survey in several parts of central Florida beginning in April 1970 revealed the distribution of C. carolina. This search indicated that the species only occurs in or near swamp habitats where the sweet-bay or white-bay tree (Magnolia virginiana) is prevalent. Experiments have indicated that this species of tree is the only food plant readily accepted by larvae of C. carolina in Florida. Other members of the family Magnoliaceae, including tuliptree (Liriodendron tulipifera) and southern magnolia (Magnolia grandiflora), failed to sustain larval growth beyond the first or second instars. A few C. carolina from South Carolina have been reared, in captivity, on tuliptree. However, it has recently been found (4) that newly hatched larvae from South Carolina, when placed on tulip-tree, died in the first instar. Thus, it seems doubtful that C. carolina ever utilizes the tulip-tree in nature.

Sweet-bay trees tend to occur, in Florida, in high-density stands that are largely isolated from one another by surrounding areas of mesic communities that lack this food plant. The moths were found to occur as isolated colonies associated with these bay swamps rather than to have a blanketing distribution through many habitats (5).

One of the most interesting behavioral features discovered regarding C. carolina is its habit of actively flying and breeding in the middle of the day; nearly all other silk moths are active during the nocturnal hours. In both captive and free-flying specimens, the males became active and flew in a search pattern beginning at about 10 a.m. and continuing for 3 to 5 hours, if no union with a female occurred. Initiation of the mating flight in males did not require any pheromone stimulation and is undoubtedly timed by an internal physiological clock. Males exhibited a very rapid and undulating flight pattern and tended to concentrate their activities at treetop heights. However, when males were following the scent of a signaling female, they exhibited a slightly slower, and more deliberate, crisscrossing flight pattern as they proceeded upwind toward the source of the attractant.

Females began signaling as early as 9:30 or 10 a.m., and continued to evert the pheromone gland at the tip of the abdomen, more or less continuously, until 2 or 3 p.m., if mating failed to occur. Females also showed a tendency to stop signaling when approached closely by fluttering males. This frequently resulted in the failure of some males to locate the female at close range. When a female did not immediately resume signaling, males usually lingered in the area and continued to search, but some quickly veered upward to the treetops and left the area as if alarmed.

It was also common for numbers of males to be attracted to a female but refuse to mate even though she continued to signal. Such males frequently flew erratically about the general area of the female for half an hour or more before departing. The reason for the failure of such males to copulate remains obscure.

After the coupling of a male and female is accomplished, they become quiet and generally remain paired for 2 to 3 hours. This is shorter than the copulation time reported for most silk moths ( $\delta$ ). A briefer union may reflect the fact that moths breeding diurnally are much more susceptible to avian predation than are nocturnally breeding ones.

Some captive females began laying eggs almost immediately after the copu-



Fig. 1. Paired male and female sweet-bay silk moths (Callosamia carolina) at midday.

lation period, while others delayed for several hours. The pearl-white eggs were deposited in small groups, and the total oviposition generally numbered well over 100 eggs. Under normal outdoor conditions, the larvae hatched 7 to 10 days after deposition.

Moths usually emerged from their cocoons during the hours between 8 p.m. and midnight. The wings expanded and dried rapidly, but no breeding flight or pheromone signaling occurred before midmorning of the following day.

On many occasions, if a signaling female was taken into a large bay swamp at midmorning, she would be almost immediately deluged by dozens of males flying from the downwind direction where none were previously visible. This attests to the abundance of the species in such areas. However, cocoons were difficult to locate in the extensive canopies of the evergreen bay trees. Also, the males were seldom observed and were virtually uncollectable when they flew at treetop height in thick swamp forests. These factors combine to falsely indicate that the species is rare, even in their prime habitat.

Most cocoons were located by laboriously examining the whitish undersurfaces of sweet-bay leaves with the aid of binoculars. The cocoons are silvery in coloration, and are found wrapped in a leaf, and usually attached to a twig by a strand of silk after the fashion of Callosamia promethea. Occasionally, cocoons were located on the green upper surface of a bay leaf, and these were much easier to locate because the silvery coloration stood out. Sweet-bay trees in Florida drop many old leaves from January to March as the new growth appears, and this proved to be the most productive time for locating cocoons. Old cocoons tended to remain attached to the tree for at least a year after the emergence of the moths.

In central Florida, the sweet-bay silk moth is double-brooded. Adults from overwintering pupae emerged in the spring between mid-March and mid-April. Their offspring did not diapause under outdoor conditions, but emerged from 3 to 6 weeks after pupation, that is, from mid-July to mid-August. The second brood diapaused and over-wintered in several groups reared in captivity. There was considerable dimorphism in the coloration of spring- and summer-brood adults; the latter, especially the males, were significantly darker

The larger larval instars of C. caro-

lina are chalky white (not slightly greenish as C. angulifera) affording protective coloration on the equally chalky white undersides of sweet-bay leaves. The larvae tended to be gregarious, especially in the early instars, but this pattern largely disappears in later instars. Few larvae survived under unsleaved conditions with both avian and hymenopterous predators being responsible for losses to larvae reared in the open. Approximately 60 percent of cocoons collected in the field had fallen prey to parasitic wasps.

Since the breeding behavior of C. carolina is so strongly diurnal, reproductive isolation from C. angulitera, which is totally nocturnal, would seem to be complete under natural conditions (7). It also does not appear to overlap the late afternoon breeding pattern of C. promethea to any great extent. Where these species overlap in their ranges, the difference in circadian activity no doubt serves as an effective isolating mechanism in otherwise reproductively compatible forms.

It is unclear whether C. carolina might be more closely related to C. promethea than C. angulifera as previously supposed, especially when one considers that the first two species are diurnal and exhibit an identical type of cocoon structure, dissimilar to that of C. angulifera. In general, insects with "complete" metamorphosis, such as moths, can be regarded as two organisms in one from the point of view of evolution. Natural selection for certain characteristics may occur in larval stages independently of differences or similarities in imagoes.

Also of great theoretical interest to moth speciation would be experiments crossing the three species of Callosamia. Interspecies matings in the genus are readily accomplished by hand-pairing methods (8) or by manipulation of the photoperiod. If the time of mating activity is genetically fixed, then when during the 24-hour cycle would hybrids of C. carolina and C. angulifera mate, or hybrids of C. carolina and C. promethea? Considerable genetic information of evolutionary significance might be obtained by a study of the behavioral patterns of these hybrid crosses of species in the genus Callosamia.

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# **Complex Components of Habitat Suitability within a Butterfly Colony**

Abstract. The microdistribution of adult Euphydryas editha changes from year to year, and the colony is subdivided into three populations that fluctuate independently in size. These observations are attributed largely to fluctuations in time and space of three complex larval resources associated with the availability of food. This complexity also entails selection pressure favoring the observed low dispersal tendency of adults.

A long-term study of the colony of the nymphaline butterfly Euphydryas editha Bvd. at Jasper Ridge (San Mateo County, California) combined measurement of poulation structure and gene flow (1) with phenetic (2), genetic, and behavioral (3) studies. It was found that (i) The colony comprises three populations, termed C, G, and H; (ii) these populations fluctuate in size independently of each other; (iii) the distribution of adult insects is variable from year to year; and (iv) the insects do not occupy all the available habitat, as defined in terms of their known resources.

Detailed ecological investigation described here reveals selection pressures that act to restrict gene flow, provides explanations for observations ii and iii above, and redefines larval resources so that observation (iv) no longer applies.

At Jasper Ridge, E. editha is a univoltine insect with a flight season usually extending from about 18 March to 22 April. The eggs are laid in masses of 20 to 350 at or close to the base of a food plant, Plantago erecta Morris (Plantaginacae). They hatch after 13 to 15 days. The young larvae feed for about 3 weeks and then enter a summer diapause which is broken in late December or January.

In 1968, the fates of 30 masses of eggs laid throughout the flight season were followed. In 23 of these, the P. erecta plants underwent senescence between the time of oviposition and hatching of the eggs, and the first instar larvae starved. No larvae from these egg masses were observed to reach the middle of third instar, the earliest stage at which larvae are capable of entering diapause if deprived of food. It was predicted that the microhabitat patches in which senescence of P. erecta occurred latest would be the areas of highest postdiapause larval density in January 1969. This prediction was not fulfilled (4).

In April and May 1969, a detailed study of population H showed that mortality of newly hatched larvae was about 80 percent. The remaining larvae could survive in three sets of circumstances.

1) The eggs are laid very early in the flight season, on Plantago erecta that will remain green for a further 5 weeks.

2) Eggs are laid on, or larvae are able to locate, P. erecta plants that have grown much larger than their fellows and that remain green for longer into the dry season, as a result of local soil tilling by gophers (Thomomys bottae) during the preceding winter.

3) Larvae are able to locate flowers of the hemiparasitic annual plant Orthocarpus densiflorus Benth. (Scrophulariaceae), on which they feed.

In each population, the degree of type 1 survival depends on the relative timing of the flight season of E. editha and the senescence of most of the P. erecta plants. This phase relation is most favorable on slopes facing north, and its variation from year to year depends in complex fashion on climatic factors (4).

Type 2 survival depends on the extent, timing, and spatial pattern of

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