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A classification system for mosquito life cycles: life cycle types for mosquitoes of the northeastern United States

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ABSTRACT: A system for the classification of mosquito life cycle types is presented for mosquito species found in the northeastern United States. Primary subdivisions include Univoltine Aedine, Multivoltine Aedine, Multivoltine *Culex/Anopheles,* and Unique Life Cycle Types. A montotypic subdivision groups life cycle types restricted to single species. The classification system recognizes 11 shared life cycle types and three that are limited to single species. Criteria for assignments include: 1) where the eggs are laid, 2) typical larval habitat, 3) number of generations per year, and 4) stage of the life cycle that overwinters. The 14 types in the northeast have been named for common model species. A list of species for each life cycle type is provided to serve as a teaching aid for students of mosquito biology. ***Journal of Vector Ecology* 29 (1): 1-10. 2004.**

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INTRODUCTION

There are currently more than 3,000 mosquito species in the world grouped in 39 genera and 135 subgenera (Clements 1992, Reinert 2000, 2001). Biological processes in a group this large show considerable variation, and a system beyond generic subdivision is needed to divide the members into logical groupings. Bates (1949) was the first mosquito biologist to categorize mosquito life cycles on the basis of shared life cycle strategies. His system recognized four temperate and four tropical mosquito life cycle types designed to separate species that bred continuously from those that utilized overwintering mechanisms. Bates named his four temperate life cycle types after well known species creating models to which students and workers could relate. Bates recognized that tropical mosquitoes breed continuously unless their development is interrupted for lack of water, and he grouped his tropical life cycle types by habitat to indirectly reflect wet vs. dry season abundance.

The world-wide classification system developed by Bates provides a template for life cycle classification but has limited value as a training tool for North American mosquito control workers. A number of mosquito species in the continental United States have unique life cycle strategies that do not fit into any of the four basic temperate types that Bates described in his book. Two of the mosquitoes he suggested as model species occur only in Europe and one of his temperate life cycle types is not utilized by any known species in the new world. As a result, Bates' system outlines an excellent life strategy model but requires extensive modification for North American applications.

Pratt (1959) recognized many of the problems with Bates' world-wide classifications and proposed an alternate system restricted to North American mosquitoes. Pratt's classification relies on three biological characteristics: 1) stage in which the mosquito overwinters, 2) place where the eggs are laid, and 3) number of generations per year. Pratt's system recognizes eleven life cycle types but is not without problems. Numerous mosquito species that enter dormancy in the north are continuous breeders further south. As a result, Pratt's system covers so broad a geographic area that the same species can exhibit as many as 3 different life cycle types over its natural range. The system is also so generalized that salt marsh floodwater, fresh floodwater and container breeding aedines are all grouped in a single life cycle type. Similarly, pristine freshwater swamp species are grouped in a life cycle type that includes brackish and polluted water breeders. The primary problem with both systems is the fact that neither author provided a complete list of species for any of the life cycle types they established. As a result, both systems are designed primarily for instructors and have limited application as independent teaching tools.

The system presented in this paper builds on Bates' life cycle types for temperate areas but subdivides each as variations on the basic themes he envisioned. In the tradition of Bates, each life cycle type is named for a common species to serve as a local model. The system utilizes Pratt's criteria as subdivisions but adds larval habitat as an additional consideration. This groups species that share larval habitat and allows more specificity in the category of where the eggs are laid. The system purposely limits life cycle classification to a specific geographic area to avoid problems posed by winter dormancy. A complete list of species for each life cycle type is provided to serve as a teaching aid for students of mosquito biology in the northeastern United States.

The life cycle classification system presented in this paper is based on a prototype originally proposed for New Jersey mosquitoes by Crans and McNelly (1997). Their system has been expanded to include the entire northeastern region and several of the New Jersey model species have been changed to reflect the range expansion. Bates' original life cycle types have been added as primary subdivisions to group all of the species in the northeast that share basic univoltine aedine, multivoltine aedine, and multivoltine *Culex*/*Anopheles* life cycle characteristics. A primary subdivision has been added for life cycle types that Bates did not mention. Life cycle types exhibited by single species have been grouped in a "Monotypic" subdivision.

Criteria for life cycle classification

Bates' type species for temperate areas included: 1) *Aedes cinereus*, a univoltine culicine that overwinters in the egg stage, 2) *Aedes caspius*, a multivoltine culicine that overwinters in the egg stage, 3) *Anopheles claviger*, a univoltine anopheline that overwinters as a larva, and 4) *Culex pipiens*, a multivoltine culicine that overwinters as a mated female.

Bates' *Aedes cinereus* life cycle type was designed to group single generation culicine mosquitoes with desiccation-resistant eggs that appear very early in the spring, a life cycle adaptation that apparently evolved for survival under arctic conditions. The eggs of this group are deposited in a variety of low-lying ground depressions where water accumulates from snow melt and spring rains. The high spring water table initiates egg hatch when water temperatures rise to levels that allow larval development to progress (Corbet 1966). Egg diapause (Clements 1997) prevents egg hatch during the summer months if the eggs are flooded by heavy summer rains. As a result, the eggs deposited by adults that emerge in early spring remain dormant for nearly a year and do not produce larvae until the following spring. Pratt (1959) had a similar life cycle type that he referred to as "Northern *Aedes*." The classification system proposed in this paper will group these mosquitoes as "Univoltine Aedines" and subdivide them by habitat type.

Bates' *Aedes caspius* life cycle type grouped multivoltine culicine mosquitoes with desiccation-resistant eggs. The eggs of this group are deposited in a variety of habitats that are flooded on an irregular basis by either rain or tide. A separate generation is produced each time the eggs are inundated during the summer months. The species in this life cycle type overwinter in the egg stage when ambient temperatures are not conducive to egg hatch and larval development (Horsfall et al. 1973). Many of the species in this group share habitat with univoltine aedines but have a higher threshold for larval development and do not hatch during early spring floodings. Pratt (1959) had a similar category that he called the "Temporary Pool *Aedes* and *Psorophora* Type." The classification system proposed in this paper will group these mosquitoes as "Multivoltine Aedines" and subdivide them by habitat type.

Bates' *Culex pipiens* life cycle type grouped multiple generation *Culex* and *Anopheles* mosquitoes that overwinter as mated females. Pratt (1959) used the same model species for the life cycle type in his classification system. This group of mosquitoes, including some members of the genera *Culiseta* and *Uranotaenia*, possesses eggs that are incapable of drying and are, thus, deposited directly on water (Hinton 1968a). Special adaptations allow the eggs to float on the surface prior to eclosion. The eggs of *Anopheles* are laid singly and possess air filled exochorionic floats. *Culex, Culiseta,* and *Uranotaenia* lay their eggs in rafts that utilize trapped air, hydrophobic areas and in some cases, hydrophilic cups to keep them on the surface (Clements 1992). The spring generation is delayed until nighttime temperatures rise to levels that allow the mated, overwintering females to host seek and oviposit. Breeding is continuous with overlapping generations during the summer months. Mated females from this group enter hibernaculae in the fall when temperatures drop and photoperiod shortens (Spielman and Wong 1973, Vinogradova 2000). The classification system proposed in this paper will group these mosquitoes as "Multivoltine *Culex* and *Anopheles*" and subdivide them by habitat group.

Bates' *Anopheles claviger* life cycle type has no counterpart in North America but several univoltine/multivoltine species do overwinter in the larval stage.

The classification system proposed in this paper will group these mosquitoes as "Unique Life Cycle Types" and will subdivide them by habitat group. Pratt (1959) recognized three life cycle types that were represented by single species. The classification system proposed in this paper will group these species as "Monotypic Life Cycles" and provide details for each of the criteria used for their classification.

Each of the groupings listed above will be categorized by the following four criteria: 1) where the eggs are laid, 2) typical larval habitat, 3) number of generations per year, and 4) stage of the life cycle that overwinters. Using these designations, the classification system recognizes 11 shared life cycle types for mosquitoes of the northeastern United States and three that are restricted to a single species (Table 1).

Univoltine aedine life cycle types in the northeastern United States

Bates' original *Ae. cinereus* life cycle type has three variations in the northeastern United States that includes: univoltine mosquito species that utilize woodland pool habitats, univoltine species found in swamps and bogs, and a group of univoltine mosquitoes that are not only generalists but frequently appear more than once during a single breeding season. The model species include *Oc. stimulans*, *Oc. abserratus,* and *Oc. canadensis*, respectively.

Ochlerotatus stimulans Type

- Desiccation-resistant eggs laid in ground depressions in wooded areas
- Larvae develop in woodland pool/snow pool habitats
- Single generation in early spring
- Overwinters in the egg stage

Ochlerotatus stimulans is the northeastern model species for single generation mosquito species that Pratt (1959) referred to as "Northern *Aedes.*" The larvae are found in a variety of leaf-lined vernal pools in wooded areas that are flooded by a combination of spring rains and snow melt. Typical larval habitats are characterized by lack of aquatic vegetation and a thick layer of leaf litter. The water is usually quite clear when the eggs first hatch but tannins from decomposing leaves progressively darken the habitat water as the larvae pass from 1st to 4th instar. The larvae of species that belong to this life cycle type must complete their development before the surrounding trees break dormancy. Trees that will later shade the habitat draw heavily on ground water as they leaf out causing rapid dry down of this transient aquatic habitat. During years when the water table is low, trapped larvae often become condensed in the leaf litter in the deepest sections of individual pools. When this occurs, pressing a dipper into moist areas can produce large numbers of larvae and pupae from a habitat that appears to be dry. Adult females of this life cycle type deposit their eggs in the band of moist leaves as the pools dry down. As the season progresses, the pools dry completely and become depressions in the forest floor. The 1st instar pharate larvae within the eggs enter diapause (Clements 1992) for the remainder of the season and do not hatch until the following spring. Nine univoltine aedines share this life cycle type in the northeastern United States (Table 1).

Ochlerotatus abserratus Type

- Desiccation-resistant eggs laid above the water line in saturated soil habitats
- Larvae develop in swamps and bogs
- Single generation in early spring
- Overwinters in the egg stage

Ochlerotatus abserratus is the northeastern model species for a group of univoltine mosquito species that are found in permanent rather than transient early spring habitats. Although most of the members are aedines, the life cycle type is shared by *Culiseta* species (subgenus *Culicella*) that have winter-hardy eggs. The larvae of mosquito species that utilize this life cycle type can be collected from a variety of bog habitats in early spring. Many of the species are adapted to specific swamp habitats such as red maple, cattail, and sphagnum swamp. Only rarely do members with this life cycle strategy share a habitat with any of the members of the *Oc. stimulans* type. Many of the mosquitoes in this group deposit their eggs within clumps of aquatic vegetation and rely on the high spring water table for inundation and egg hatch. The larvae become sparsely distributed in heavily vegetated areas of the swamp and are only infrequently collected close to the shoreline. The univoltine mosquitoes in this group appear somewhat later in the season than univoltine transient water species. Many of the bog breeding univoltine species in this group do not appear as larvae until the trees begin to leaf out. They usually reach highest population levels well after transient habitats have dried completely. Ten univoltine culicines share this life cycle type in the northeastern United States (Table 1).

Ochlerotatus canadensis Type

- Desiccation-resistant eggs laid in a variety of transient and permanent water situations
- Larvae develop in a wide variety of freshwater habitats

- Major generation in early spring followed by sporadic egg hatch later in the season
- Overwinters in the egg stage

Ochlerotatus canadensis is the northeastern model species for a small group of mosquitoes, generally listed as single generation, that often appear more than once during a single breeding season. Larvae that hatch in early spring make up the bulk of the population, but one or more overlapping cohorts often follow during the spring months. In some years, the species that utilize this life cycle type reappear in numbers if heavy rains re-flood the habitat in late summer and early fall. Most authors attribute the sporadic hatch to a single generation of overwintering eggs that require more than one flooding (Matheson 1944). Three, presumably univoltine species, share this life cycle type in the northeastern United States (Table 1). The model species, *Oc. canadensis,* is a transient water breeder that utilizes a wide range of early spring habitats but also oviposits in leaf litter along the margins of more permanent bodies of water. *Ae. cinereus* is a bog breeder that occasionally appears in woodland pools. *Oc. sticticus* is a late spring species that reaches highest numbers on floodplains, particularly in shaded woodland pools along the margin of large river systems.

Multivoltine aedine life cycle types in the northeastern United States

Bates' original *Ae. caspius* life cycle type has three variations in the northeastern United States that include: multivoltine aedines that utilize fresh floodwater habitats, multiivoltine aedines with a high degree of salt tolerance, and multivoltine aedines that breed in container habitats. The northeastern model species include *Ae. vexans*, *Oc. sollicitans,* and *Oc. triseriatus*, respectively.

Aedes vexans Type

- Desiccation-resistant eggs laid in ground depressions inundated by fresh floodwater
- Larvae develop in a wide range of transient freshwater habitats
- Multiple generations each year
- Overwinters in the egg stage

Aedes vexans is the northeastern model species for a group that includes multivoltine mosquitoes in the genera *Aedes, Ochlerotatus,* and *Psorophora.* The members of this group rely on summer rains to flood eggs that are deposited in low-lying ground depressions and are commonly referred to as floodwater mosquitoes (Horsfall et al. 1973). Flood plains where rivers overflow their banks generate the highest populations but significant numbers can be produced from virtually any area where fresh ground water accumulates on an intermittent basis. The entire group undergoes accelerated larval development and can pupate four to five d after egg hatch when ambient temperatures are favorable. A number of species in this group prefer shaded larval habitats and emanate from the same woodland pools that produced univoltine aedines in early spring (Means 1979). Most members in the group, however, deposit eggs in ground depressions exposed to direct sunlight and rely on high daytime temperatures to accelerate completion of their larval development before the habitat dries down. None of the mosquitoes in this group have salt tolerance. Sixteen species from three genera are included in this life cycle type in the northeastern United States (Table 1).

Ochlerotatus sollicitans Type

- Desiccation-resistant eggs laid on a substrate periodically flooded by lunar tides
- Larvae develop in salt marsh pools
- Multiple generations each year
- Overwinters in the egg stage

Ochlerotatus sollicitans is the northeastern model species for a group of floodwater mosquitoes with a high degree of salt tolerance. Multivoltinism combined with salt tolerance allows these mosquitoes to utilize vast expanses of salt marsh wetlands as larval habitat unsuitable to other floodwater species. The eggs are normally deposited in ground depression on marshland that is high enough to exclude daily tide cycles. The positioning allows eggs to be flooded by lunar tides producing two broods at roughly two-wk intervals during the summer months. Additional broods can be triggered by storm tides or heavy summer rains if enough time has elapsed after oviposition for embryonation and formation of the serosal cuticle (Harwood and Horsfall 1959, Clements 1992). Four species with this life cycle type are found in the northeastern United States (Table 1). *Oc. cantator* is an early season species found as larvae in greatest numbers on the upland edges of the salt marsh in April and May. *Oc. sollicitans* and *Oc. taeniorhynchus* are summer mosquitoes that move off the marsh as adults in large numbers for a bloodmeal host (Smith 1904, Provost 1952). *Oc. dorsalis* is a common western species that is relatively rare in the northeastern United States.

Ochlerotatus triseriatus Type

- Desiccation-resistant eggs laid above the water line in container habitats
- Larvae develop in a wide range of natural and artificial containers
- Multiple generations each year
- Overwinters in the egg stage

Table 1. Life cycle types for mosquito species found in the northeastern United States.

Univoltine Aedine Life Cycle Types	Multivoltine Aedine Life Cycle Types	Culex/Anopheles Life Cycle Types	Unique Life Cycle Types	Monotypic Life Cycle Types
Oc. stimulans **Type** *Oc. stimulans* *Oc. communis* *Oc. excrucians* *Oc. grossbeckii* *Oc. impiger* *Oc. implicatus* *Oc. intrudens* *Oc. provocans* *Oc. punctor*	***Ae. vexans*** **Type** *Ae. vexans* *Ps. columbiae* *Oc. atlanticus* *Ps. ciliata* *Oc. dupreei* *Ps. discolor* *Oc. flavescens* *Ps. cyanescens* *Oc. infirmatus* *Ps. ferox* *Oc. mitchellae* *Ps. horrida* *Oc. spenceri* *Ps. howardii* *Oc. trivittatus* *Ps. varipes*	***An. quadrimaculatus*** **Type** *An. quadrimaculatus* *An. earlei* *An. perplexens** *Ur. sapphirinna* *Cx. erraticus* *Cx. territans*	***Cs. melanura*** **Type** *Cs. melanura* *An. crucians*	***Cq. perturbans*** **Type** *Cq. perturbans*
Oc. abserratus **Type** *Oc. abserratus* *Oc. aurifer* *Oc. decticus* *Oc. diantaeus* *Oc. fitchii* *Oc. pionips** *Oc. riparius** *Oc. thibaulti* *Cs. minnesotae* *Cs. morsitans*	***Oc. sollicitans*** **Type** *Oc. sollicitans* *Oc. cantator* *Oc. dorsalis* *Oc. taeniorhynchus*	***Cx. salinarius*** **Type** *Cx. salinarius* *An. bradleyi* *An. atropos*	***Or. signifera*** **Type** *Or. signifera* *Or. alba* *An. barberi* *Tx. rutilus septentrionalis*	***An. walkeri*** **Type** *An. walkeri*
Oc. canadensis **Type** *Oc. canadensis* *Ae. cinereus* *Oc. sticticus*	***Oc. triseriatus*** **Type** *Oc. triseriatus* *Oc. hendersoni* *Oc. atropalpus* *Oc. japonicus* *Ae. albopictus*	***Cx. pipiens*** **Type** *Cx. pipiens* *Cx. restuans* *Cx. tarsalis* *Cs. inornata* *Cs. impatiens* *An. punctipennis*		***Wy. smithii*** **Type** *Wy. smithii*

* Only limited information is available to accurately assign this species to a life cycle type in the northeastern United States.

Ochlerotatus triseriatus is the northeastern model species for a group of floodwater mosquitoes that develop in container habitats. The species within this group deposit their eggs in bands just above the waterline in containers that regularly receive rainwater (Newkirk 1955). Evaporation provides additional oviposition substrate while rainfall raises the water level stimulating egg hatch. Treeholes, plant axils, and rock pools are natural container habitats utilized by members of this group. Discarded tires and a wide array of artificial containers provide additional habitat if the containers hold enough decomposing plant material to mimic natural sites (Means 1979). Five species with this life cycle type are found in the northeastern United States (Table 1). *Ochlerotatus triseriatus*, the model species, is relatively common in suburban areas but reaches greatest numbers where discarded tire piles provide abundant breeding habitat. *Aedes albopictus* and *Ochlerotatus japonicus* are exotics that were probably introduced by the practice of importing used tires for re-treading purposes (Eads 1972, Sprenger and Wuithiranyagool 1986).

Multivoltine *Culex* and *Anopheles* life cycle types in the northeastern United States

Bates' original *Cx. pipiens* life cycle type has three variations in the northeastern United States that include: continuous breeders that utilize pristine freshwater swamp habitats, continuous breeders that utilize brackish water habitats, and continuous breeders that thrive in polluted water habitats. The northeastern model species include *An. quadrimaculatus*, *Cx. salinarius,* and *Cx. pipiens*, respectively.

Anopheles quadrimaculatus Type

- Non desiccation-resistant eggs laid directly on water in pristine freshwater habitats
- Larvae develop in freshwater swamps and bogs
- Multiple generations each year
- Overwinters as a mated female

Anopheles quadrimaculatus is the northeastern model species for a group of mosquitoes that hibernate as mated females and deposit non desiccation-resistant eggs in freshwater swamps and bogs. Typical breeding habitat supports abundant aquatic vegetation (Horsfall and Morris 1952). The members of this life cycle type typically replace the bog breeding univoltine aedines in the *Oc. abserratus* life cycle type as the season advances. Larvae from this group do not appear until evening temperatures allow the hibernating adults to exit hibernaculae, seek a host, and oviposit. Larval populations are typically sparse in late spring, build progressively during the summer and do not peak until mid-summer or early fall. Six species from three genera in this life cycle type are found in the northeastern United States (Table 1).

Culex salinarius Type

- Non desiccation-resistant eggs laid directly on water in brackish water habitats
- Larvae reach greatest numbers in brackish water swamps
- Multiple generations each year
- Overwinters as a mated female

Culex salinarius is the northeastern model species for a group of multivoltine *Culex/ Anopheles* that exhibit some degree of salt tolerance. This life cycle type is the non-aedine counterpart of the *Oc. sollicitans* life cycle type. The eggs, however, are deposited directly on standing water rather than on moist mud in habitats that are flooded by lunar tides. Although they are often called salt marsh mosquitoes, the species in this group rarely breed directly on tidal marshes (Dyar and Knab 1906). Most reach greatest abundance in areas adjacent to salt marshes where fresh water from the upland drains on to coastal habitats producing a brackish water environment. Each of the species in this group is capable of breeding in freshwater habitats but reaches greatest concentrations in areas close to the coast. Slaff and Crans (1982) showed that freshwater impoundments were a major producer of the members of this life cycle type in coastal areas of New Jersey. Murphey and Burbutis (1964) showed that members of this group were highly attracted to chemical volitiles from infusions created by salt marsh vegetation die off when marshland is flooded with fresh water. Three species in this life cycle type are found in the northeastern United States (Table 1).

Culex pipiens Type

- Non desiccation-resistant eggs laid directly on water with high organic content
- Larvae thrive in polluted water habitats
- Multiple generations each year
- Overwinters as a mated female

Culex pipiens is the northeastern model for a group of multivoltine *Culex/Anopheles* with pollution tolerance. Typical breeding habitat requires water with high organic content. Rotting vegetation, decaying animal wastes, and septic seepage are highly attractive to the mosquitoes included in this group. Catch basins, sewer treatment plants, and landfills provide typical ground water habitat. Members that utilize this life cycle type will also lay their eggs in artificial containers that hold putrid water.

The gravid trap developed by Reiter (1983) relies on fermented infusions as an attractant specifically for the members of this group. Six species from three genera in this life cycle type are found in the northeastern United States (Table 1).

Unique life cycle types in the northeastern United States

A number of North American mosquito species do not logically fall into any of Bates' original life cycle types. Those that overwinter in the larval stage require modification of the univoltine life cycle type that Bates modeled after the European species, *Anopheles claviger*. *Culiseta melanura* and *Orthopodomyia signifera* are multivoltine culicines that can be used as models. The former represents multivoltine culicines that overwinter as larvae in freshwater swamps. The latter represents multivoltine culicines that overwinter as larvae in container habitats.

Culiseta melanura Type

- Non desiccation-resistant eggs laid directly on water
- Larvae develop in swamps and bogs
- Multiple generations each year
- Overwinters in the larval stage in typical freshwater swamp habitats

Culiseta melanura is the northeastern model species for multivoltine freshwater swamp breeders that overwinter in the larval stage. Pratt (1959) proposed a similar life cycle type named after the same model. The larval stage of the members of this life cycle type become quiescent during the winter months and burrow into the bottom sediment. Fourth instar larvae generally predominate but earlier instars frequently make up a portion of the overwintering population (Burbutis and Lake 1956). Frohne and Hart (1949) described this overwintering mechanism for *An. crucians* in the southern United States. Mahmood and Crans (1998) studied cold tolerance in *Cs. melanura* and determined that the species is probably bivoltine in parts of its range. These two species are the only representatives of this life cycle type in the northeastern United States (Table 1).

Orthopodomyia signifera Type

- Non desiccation-resistant eggs laid on water in container habitats
- Larvae develop in natural and artificial containers
- Multiple generations each year
- Overwinters in the larval stage

Orthopodomyia signifera is the northeastern model species for multivoltine container breeders that overwinter in the larval stage. The entire group behaves somewhat like sabethines but are widely distributed in the northeastern United States. The eggs of members of this group are deposited directly on the water's surface (Horsfall 1955). Howard et al. (1917) reported that some eggs of the model species, *Or. signifera*, adhere just above the waterline allowing newly-hatched larvae to slide down into the habitat water. Breeding is continuous during the summer months. The larvae burrow into the bottom sediment during the winter and pupate the following spring (Lake 1954). The life cycle type appears to be adapted for treehole habitats where the flocculent bottom sediment provides protection from freezing. Specimens that attempt to overwinter in artificial containers usually freeze solid and suffer extensive winter mortality (personal observation). Four northeastern species from three genera share this life cycle type (Table 1).The list includes *Toxorhynchites rutilus septentrionalis*, a predacious temperate Toxhorhynchitine (Darsie and Ward 1981) that preys readily on container breeding culicines in southern portions of the northeastern United States.

Monotypic life cycle types in the northeastern United States

A number of the mosquito species found in North America possess biological characteristics that make them the only representative of a distinctive life cycle type. Northeastern species that fall into this category include *Coquillettidia. perturbans*, *Anopheles walkeri,* and *Wyeomyia smithii*.

Coquillettidia perturbans Type

- Non desiccation-resistant eggs laid directly on water
- Larvae attach to the roots of aquatic vegetation in freshwater swamps
- One extended generation each year
- Overwinters in the larval stage

Coquillettidia perturbans is a mosquito with larvae and pupae that possess a unique respiratory apparatus that enable them to extract oxygen directly from the roots of submerged aquatic plants (Bosak and Crans 2002). The species lays its eggs in rafts (Hagmann 1953) that are somewhat similar in structure to those of *Culex*, *Culiseta,* and *Uranotaenia*. Overwintering takes place in the larval stage in any instar trapped by the onset of winter. The life cycle is unique because they take one full year to complete a single generation in the northeastern United States. Adult emergence appears to occur in broods over the course of the summer but actually represents cohorts of larvae that passed the winter in different instars. Members of the genus

Mansonia in the southern United States have similar larvae and pupae but attach their eggs to the underside of floating leaves and have a life cycle that is not interrupted by winter dormancy.

Anopeles walkeri Type

- Non desiccation-resistant eggs laid directly on water
- Larvae develop in freshwater swamp habitats
- Multiple generations each year
- Overwinters in the egg stage

Anopheles walkeri is a multivoltine North American anopheline that overwinters in the egg stage. Hurlbut (1938) showed that the species possesses a winter hardy egg that differs from summer eggs by having enlarged floats that nearly cover the dorsal surface of the exochorion. Overwintering in the egg stage extends the seasonal cycle of this species by allowing it to pass through one full larval generation before ambient temperatures allow hibernating females of other anophelines to become active. The first generation shares freshwater swamp habitat with bog-breeding univoltine aedines as well as *Culiseta* of the subgenus *Culicella* when early spring vegetation is still sparse. Because *An. walkeri* is multivoltine, it remains after the swamp becomes weed choked and shares habitat with members of the *An. quadrimaculatus* life cycle type.

Wyeomyia smithii Type

- Non desiccation-resistant eggs deposited in pitcher plants
- Larvae develop only in leaves of the pitcher plant, *Sarracenia purpurea*
- Multiple generations each year
- Overwinters in the larval stage

Wyeomyia smithii is the only sabathine mosquito species found in the northeastern United States (Darsie and Ward 1981). Adult females deposit rhomboid-shaped eggs in the pitcher plant, *Sarracenia purpuria,* beginning in early spring, and multiple generations of larvae feed actively on the carcasses of insects that are trapped and dissolved by the predacious host plant (Istock et al. 1975). Larvae remain in the plant during the winter months, often frozen within a solid block of ice (Smith 1902). Larval growth and development is suspended during the winter months and resumes with the advent of warmer weather.

DISCUSSION

The classification system presented in this paper is designed primarily as a teaching tool for students of mosquito biology. Students are encouraged to collect and identify larval specimens from the field and use the information presented here to understand life cycle characteristics of the specimens in their possession. The life cycle types have been named after common local models to provide associations for species that share habitats and are frequently collected together. The system is designed to encourage habitat recognition together with seasonal distribution and can, therefore, be used to identify potential habitats for species that are rare and seldom encountered. The system should also be useful to help train biologists and inspectors of mosquito abatement districts. A firm knowledge of the basic biology of individual species is essential for responsible mosquito control decisions.

Similar classification systems can, and should be, developed for other geographic areas. In the northern half of the United States, the basic life cycle types will be similar, but local model species should be substituted for teaching purposes. Changes will be required for life cycle types in the southern United States where breeding is not interrupted by periods of cold weather. In arid areas, a category to include species that aestivate as adults might be useful. Bates (1949) did propose tropical life cycle types in his book for species that did not overwinter. His classification system included categories for: 1) Permanent and Semipermanent pool *Anopheles* and *Culex* that breed continuously, 2) Anopheline species that are stream breeders, 3) Temporary pool species that appear after rain events, and 4) Multivoltine container breeding species, including the *Sabethines*, *Haemagogus* and certain *Aedes*. Bates did not have a category for tropical crab hole breeders. For consistency, classification systems for southern regions should rename the categories of Bates after local model mosquito species that utilize typical habitats. Because breeding is continuous, the criteria used for subdividing these mosquitoes would exclude the stage of the life cycle that overwinters. The "number of generations per year" category would separate continuous breeders with overlapping generations from those that appear in broods.

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