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Roger D. Moon
University of Minnesota, St. Paul

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ROGER D. MOON*

ABSTRACT — The 51 species of mosquitoes known to occur in Minnesota share many biological attributes. They develop through seven life stages: an egg, four larval instars, a pupa, and an adult. Females lay eggs either on water or in substrates likely to be submerged later. Larvae and pupae occur in still, shallow water. Habitats vary among species and include treeholes, temporary snowmelt pools, rainpools, semi-permanent marshes, ponds, and riverside lagoons. Duration of the stages can be affected by diapause, temperature, and nutrition. Many species overwinter as dormant eggs, while some overwinter as larvae and others as diapausing females.

The larvae of most species harvest bacteria, algae, plankton, and detritus. A few exceptional species prey on other mosquito larvae. Pupae do not feed. Larvae and pupae obtain some of their required oxygen from the water through their skin but the majority comes from the water surface. Growth and metamorphosis are orchestrated by a complex neuroendocrine system. Survival to adult is affected by weather and natural enemies.

Females of most species require vertebrate blood to produce their eggs. Males do not feed on blood. Few of the Minnesota species are strictly host specific. The majority will feed on whatever warm-blooded hosts are available. Both sexes also eat plant nectar which contributes to their 2-10 week longevity and ability to fly. Some species seem able to disperse on the wind for dozens of kilometers. Others are comparatively sedentary.

Introduction

Mosquitoes have long been a prominent part of the Minnesota experience. An early surveyor noted in his diary,

> Life (in this township) is almost unindurable (sic), from the torture of insects, and physical discomforts. I have been stung by mosquitoes . . . while standing in snow knee deep.

More seriously, mosquitoes have been the subject of scientific study since Otto Lugger, the first Agricultural Experiment Station entomologist in Minnesota, began collecting and describing the state's insects in 1888.

In the space allotted here, I will present a brief overview of mosquito biology, paying particular attention to the life history, physiology, and ecology of our fauna. My hope is that discussion of today's "biting issue" will be anchored in a good understanding of the biology of the main antagonists, the biters themselves. The interested reader will find Harwood and James (1) to contain a good general review of mosquito biology.

The Minnesota Mosquito Fauna

Minnesota can be divided into three major biogeographic regions based on geology, hydrology, and original plant communities. A diagonal line from the northwest to southeast roughly separates land that was once prairie to the west and southwest from land that is still coniferous forest in the north and northeast. The transition zone between the two is mixed, consisting of open grassland scattered among areas of deciduous and coniferous woodlands. Of course, human activity has greatly modified the landscape, but the old pattern remains visible today.

Owen (2) presented distribution maps of 34 species of mosquitoes known in Minnesota in 1937. Although the record needs updating, his maps suggest that about two-thirds of our species occur exclusively in the transition and coniferous zones. Another fifth occurs exclusively in the plains, and the remaining species are either present in all regions or rare and localized.

At latest count, 51 species in 9 genera are known to be present in our state (Table 1) (3). Forty-two are known to bite man and other vertebrates. Identifying mosquitoes is no simple task. Several of our pest species are indistinguishable as adults. Although no two mosquito species are biologically identical, they do have many features in common.

Biology of Immature Stages

Metamorphosis

All mosquitoes develop through seven life stages consisting of an egg, four larval instars, a pupa, and an adult. This kind of development is called complete metamorphosis. From egg to adult, each stage is separated from the next by the formation of a new exoskeleton and the shedding of the old exoskeleton. This process is called molting and is common to all animals with exoskeletons.

Metamorphosis is orchestrated by a complex neuroendocrine system. Each molt is initiated by release of a hormone,

*Department of Entomology, University of Minnesota, St. Paul, MN

Table 1. Taxonomic summary of the mosquito fauna of Minnesota. Abstracted from Darsie and Ward (3).

Genus	Total no. species	No. that bite mammals
Aedes	28	26
Anopheles	5	4
Coquillettidia	1	1
Culex	6	5
Culiseta	4	2
Psorophora	4	4
Others	3	3
Total	51	42

appropriately called molting hormone. Once released, molting hormone stimulates growth and activity of cells underlying the insect's skin. The net result is secretion of a new skin and digestion part of the old skin. Nerves and muscles are then coordinated when the insect crawls out of its old skin.

The form of the new skin is governed by a second hormone, called juvenile hormone (JH), whose natural concentration decreases with each successive instar. JH reaches its lowest concentration at the larval-pupal molt. One pesticide in wide use today, called methoprene or Altosid, artificially increases the concentration of JH and ultimately disrupts molting from the fourth larval instar to the pupa. As formulated for use in mosquito control, methoprene is not toxic to humans and wildlife but is thought to be selectively toxic to mosquito larvae and other closely related flies.

Eggs

Every mosquito begins its life as an egg. Eggs in the genera *Aedes* and *Psorophora* are laid singly within cracks of moist soil located in an area that is likely to be inundated at a later time. The *Anopheles* egg is also laid singly but directly on standing water. Eggs in the genera *Culex, Culiseta,* and *Coquillettidia* are also laid directly on water but in batches rather than singly.

Egg location can be correlated with egg morphology. Eggs laid singly in soil are especially resistant to drying. The *Anopheles* egg has a specialized float apparatus which keeps the egg on the surface and properly oriented. Floatation can also be imparted by the shape of a batch.

Larval habitat

In all cases, mosquito larvae and pupae occur in still, shallow water. They are most often associated with vegetation and submersed plant debris. Mosquitoes occur in a variety of aquatic habitats. A given body of water, regardless of size and permanence, may yield several species of mosquitoes. The presence of a species in a given habitat is determined largely by the behavior of the egg-laying female (4).

Some species are rather exacting and are found only in a narrow range of habitats. For example, *Aedes triseriatus,* the vector of the virus that causes LaCrosse encephalitis, occurs only in treeholes and man-made containers such as old tires, coffee cans, etc. Another rather habitat-specific species is a cattail mosquito, *Coquillettidia perturbans.* As implied by its common name, larvae are almost exclusively found in association with floating roots of cattails, *Typha* spp.

Many of our other species are found in a wider range of aquatic habitats. *Aedes vexans* is the dominant summertime nuisance mosquito in the unforested parts of the state. This species occurs everywhere from riverine floodwaters and natural rainpools to roadside ditches and even potholes and road puddles. The so-called spring *Aedes,* a group of 7 to 12 late spring pests, tends to predominate in snowmelt pools associated with deciduous and coniferous woodlands.

Larval nutrition

Detailed knowledge of larval nutrition is lacking. It is thought that larvae ingest particulate matter — bacteria, algae, plankton, and detritus. These substances can be seen in their intestines. Larval mouthparts consist of hairs, brushes, scrapers, and appendages used to filter floating particles or to scrape plant or other benthic surfaces. A few exceptional species prey on other soft-bodied invertebrates, including other mosquito larvae. Pupae do not feed.

Respiration

Larvae and pupae obtain oxygen in two different ways. A limited amount of their requirement is absorbed from the water across their skins. They obtain a far larger amount from the air directly at the water's surface. Insects lack lungs like those that vertebrates possess. Instead, every cell in an insect's body is connected to the outside world via a branched network of hollow trachae.

Mosquito larvae and pupae have respiratory siphons that conduct oxygen from the air into their respiratory system. The siphons also conduct carbon dioxide outward. The siphons have water repelling hairs that are used to break the water's surface tension. The old practice of oiling water to kill mosquitoes worked by preventing the mosquitoes from breathing at the surface.

Because food is at the benthos and air is at the surface, almost all of our species must swim and float back and forth between the benthos and surface to feed and breathe. One contrary specialization is found in the cattail mosquito. It gets all its oxygen directly from submerged plant roots and never needs to surface to get air.

Survival to adult

Survival from egg to adult is governed by a number of factors depending on the habitat and species of mosquito. Eggs can freeze, dry out, become infected with parasitic microorganisms, or be eaten by predators. Larvae and pupae will be killed if their habitat dries up, gets too hot, or gets too cold. They can also be killed by a wide variety of mosquito pathogens, including bacteria, protozoa, fungi, and worms.

And of course, mosquito larvae and pupae are food for an immense variety of other animals. These predators include other insects, worms, amphibians, fish, and waterfowl. The overall level of survival to adult in a given body of water can be greatly affected by weather and other organisms, but careful studies in our region have not been carried out to measure the significance of any of these mortality factors.

Developmental time

The time required to develop from egg to adult also varies among mosquito species and habitats and ranges from as little as six days to several years. Many of the *Aedes* eggs become dormant, perhaps in diapause, and will require wetting and rewetting to hatch. Some eggs of *Aedes vexans* have remained dormant and viable for more than three years (5). The spring *Aedes* require a period of chilling, normally over the winter, before they hatch with the spring snow melt.

Dormancy aside, it is well established that warm temperatures accelerate development in cold-blooded animals. Mosquito larvae and pupae can govern their temperature to a slight extent by moving within their habitat. Nevertheless, developmental times for chosen species, stages, and habitats can be predicted if one knows the temperature of their habitat. For example, developmental times for *Aedes vexans* can range from less than nine days at 25°C to more than 46 days at 10°C (6). Food supply for the larvae can also affect time to adult. Starvation will delay their emergence, but it is not known how often this occurs naturally.

Biology of Adults

The final and perhaps most familiar mosquito life stage is the adult. It emerges from the pupa by crawling from the pupal case at the water's surface and flying to a nearby site to rest and harden its skin. Thereafter, no more development is visible from the outside. Variation in size and color among adult mosquitoes is a property of the species and not due to growth or age after emergence.

Behavior, longevity, and movement

Adults are either male or female, and their ratio at emergence is 1:1 in most cases. They mate within a few days, and from then on both sexes spend the remainder of their lives alternately secluded in vegetation, flying to locate food, feeding, and in the case of females, laying eggs. Longevity varies with species and season. Several *Culex* and *Anopheles* overwinter as females in diapause and may live five months or more. Most mosquitoes live on the order of 2-10 weeks (7).

Flight activity is usually restricted to certain periods of the day and night, with some species being active at daytime and others active only at dusk or into the night. It appears that both sexes require regular meals of plant nectar and other carbohydrates to fuel flight and general metabolism (8,9).

Both sexes also seem to be extremely susceptible to desiccation. Only on the most humid of days will some species venture out of vegetated harborage areas. Perhaps the needs for humid microhabitats and plant nectar can explain why mosquitoes may be scarce in open terrain and at the same time be extremely numerous five paces into adjacent woods.

Long distance movement of mosquitoes is a particularly relevant but intractable subject to study in the field. Horsfall (5) argued that *Aedes vexans* is one of the more mobile species. Other species have been described as being relatively sedentary, rarely venturing far from their breeding sites. Workers have marked and released thousands of adults only to retrap dozens in succeeding weeks. Brust in Winnipeg (10) has done the most extensive work on *Aedes vexans*. He marked, released and then recaptured females as far as 11 km downwind from release points after several cool nights, but the majority (50% of all recaptures) had dispersed only 2 km. He noted that dispersal would likely be greater during warmer weather.

The need for blood

Mosquitoes would be beneficial insects were it not for their blood feeding habits. Their need for blood renders them the greatest health hazard worldwide because of their critical role as vectors of pathogenic viruses, protozoa, and nematodes (1,7). In Minnesota, two species vector two encephalitis viruses, one each. However, when compared to the rest of the world, we are at relatively low risk of becoming infected by any biting mosquito. On the other hand, leisure time outdoors at dusk is regularly cut short by biting mosquitoes. We are now beginning to question the overall impact of mosquitoes on the quality of life for residents and tourists, for our pets, for animal agriculture, and for the health of wildlife.

It should be understood that only female mosquitoes are the problem. Males do not consume blood or even orient around man and other animals. To be correct, when you swat a biting mosquito, you kill "her" not "him!" Female mosquitoes convert vertebrate blood into eggs. From the time of mating, they develop through reproductive cycles, alternately taking a blood meal and then laying eggs several days later. A few exceptional species are able to lay eggs without blood meals, and the few species that diapause as adults may not feed until diapause ends after winter. The process of finding a host is complex and modestly understood. There is evidence that mosquitoes employ vision and other abilities to detect a host's heat and aroma to locate a source of blood (11).

Analysis of blood in the guts of trapped females in the wild shows that few mosquito species are strictly host specific. Most will feed on whatever vertebrates are available, including man, pets, livestock, and wildlife. It may not be comforting to the pestered recreationer, but it is nevertheless true, that livestock, pets, and wildlife in roughly that order host many more mosquitoes than does man.

Conclusions

This brief sketch of mosquito biology does a disservice to the biological complexities of our fauna and to the depth of existing knowledge about them. Much as been sacrificed for the sake of brevity. Despite these shortcomings, I hope it is abundantly clear that mosquito populations are complex and every species is ecologically unique. An attempt to manage any of them beyond what is being done at present in the metropolitan area will require a comprehensive understanding of which species are causing the problems, where they are breeding, and what mechanisms govern their abundance and distribution.

If researchers can find mosquito control methods that are practical, inexpensive, and environmentally acceptable, decisions to use them will be based ultimately on economics. The societal benefits of successfully reducing mosquito abundance must exceed the costs, both direct and indirect. I am certain that succeeding essays in this volume will draw out many other facets of the problem. The "biting issue" is an extremely complex one. To reach a consensus will tax the abilities of biological, physical, and social scientists as well as the abilities of our politicians.

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