The Biology of Northern Mosquitoes

By W. C. FROHNE, Ph.D.

I N the last 10 years, northern Canada and Alaska, the continent's northwestern defense front, have witnessed a construction boom. In this mosquito-infested arctic wilderness, military bastions, power dams, and metallurgical plants are being erected, and oil fields and mines are being developed. A major handicap to this growth has been the seasonal swarming of mosquitoes.

Both the Canadian and United States Governments have directed scientific studies of these insects to establish their importance to public health and to improve the contributions of entomology to polar medicine.

Canadian entomologists and personnel of the Arctic Health Research Center have pushed back the frontiers of Alaskan insect lore and have provided basic biological contributions to knowledge of mosquitoes. A few years ago they discovered a hitherto unrecognized type of life cycle characteristic of many arctic mosquitoes. This discovery will serve, in conjunction with another well-known cycle, as a framework for this discussion.

The role of the northern biting Diptera, including mosquitoes, as disease vectors is largely unexplored. No one has undertaken even a pioneering general survey of pathogens associated with northern mosquitoes. Polar medical entomology today is reminiscent of the status of tropical medical entomology 60 years ago. However, studies of mosquito-borne encephalitis are progressing in Saskatchewan. In Sweden, Aedes cinereus, a mosquito abun-

Dr. Frohne is chief, Entomology Activities, Arctic Health Research Center, Public Health Service, Anchorage, Alaska. dant in Alaska as well, was recently shown to spread tularemia. Also, in subarctic Siberia, Russians have demonstrated that mosquitoes transmit malaria and Japanese B encephalitis.

Research on disease agents associated with man and mosquitoes in the far north might reveal important pathogenic counterparts to those in temperate and tropical zones, including many only recently detected. However, at present, northern Diptera are regarded primarily as biting, bloodsucking pests.

Northern Biting Insects

In Alaska and other northern countries, the Diptera include the most offensive insect species. Of all bloodsuckers, the more than two dozen mosquito species are the worst.

We omit lesser offenders, of which the major groups are: (a) Heleidae, punkies or no-seeums, about 12 species, half of them undescribed, of the genus *Culicoides*; (b) Simuliidae, or blackflies, of 36 described species; (c) Leptidae, or snipeflies, 2 redoubtable, little-known species of *Symphoromyia* resembling horseflies; (d) Tabanidae, horseflies and deerflies, an uncertain number of forms, perhaps 20. Like the better known mosquitoes, the punkies and flies are important because the females bite man.

Need for Mosquito Control

Following the lead of military medicine, and especially the counsel of the late Dr. Joseph Mountin of the Public Health Service, health workers accept mosquito abatement as adjuvant public health. Culicidology is one of the acknowledged health sciences.

During Alaska's summer, hordes of mosqui-

This welcome article brings together diverse information, some of it quite new, about the insect fauna of the far north, more information than has been assembled in one place before. It also highlights the paucity of our knowledge about these species, which are such powerful deterrents to the development of Alaska and which must be subdued if the natural resources of that vast land are to be exploited.

Virtually nothing is known about the disease-vectoring potentialities of arctic biting insects. Indeed, little has been learned about their feeding habits. It seems unlikely that the insects could transmit disease unless they engorged with blood at least twice, with the last feeding upon man. Single broodedness seems to be the rule among the northern mosquitoes. This suggests the probability of single feedings. Yet some of the mosquitoes live more than a year, and it would seem necessary for them to have more than one blood meal to sustain

normal metabolic activities even though much of the time is spent in hibernation. Probably many, if not all, hematophagous species do feed more than once.

But whether these creatures spread disease from lower animals to man, or from man to man, or whether they have nothing whatever to do with spreading disease, their overpowering numbers and vicious biting habits make insect control an almost necessary prelude to land development. To imply that they are unimportant from a health standpoint simply because they are not known to transmit infectious organisms is to discredit the basic tenet of the World Health Organization Charter. Thus, insect control becomes an essential function of health organizations in bringing about relief from severe insect pestiferousness.

—By Justin M. Andrews, Sc.D., associate chief for program, Bureau of State Services, Public Health Service.

toes attack every exposed warm-blooded animal. Certain mammals, for example the caribou, make long annual migrations to escape them. As for man, it may well be that mosquitoes more than maladies have impeded settlement of the vast and beautiful Alaskan central valleys blessed with fish, timber, and cultivable soil.

In accordance with an ecologic principle that toward the poles species increase quantitatively but decrease qualitatively, myriads of mosquitoes of a few arctic kinds attain densities rarely approached in warmer parts of the world. Man survives the polar winter by protecting himself from frost, the summer, only by antimosquito measures. Evidently, scientific control of arctic mosquito pests is needed to facilitate orderly development of Alaskan resources.

Life Cycle Types

To compare arctic mosquitoes with those in warmer latitudes, it is unnecessary to present the customary annotated list introducing the 20-odd Aedes, 5 or 6 Culiseta, 1 Anopheles, and 1 Culex which comprise the Alaskan mosquito

fauna. Someone might be misled by apparent similarities of the Alaskan assemblage of species to stateside lists. The Alaskan list is a selected biota of peculiarly cold-tolerant forms. All belong to one or the other of two dissimilar types of northern life cycles.

Alaskan mosquitoes are invariably single brooded; there is but one generation per year. The three many-brooded life cycles characteristic of almost all mosquitoes of the United States do not occur at all, so far as is known, in the Territory.

The members of a life cycle type resemble each other in essential habits, but the species do not necessarily belong to the same genus. However, one of the northern life cycles does comprise all the species of *Aedes*. The other includes a taxonomic miscellany of the three other genera. It is sound ecology and helpful toward understanding their biologies to classify the mosquitoes by life cycle type rather than to view them as a list of scientific names.

The Culiseta impatiens type of life cycle was recognized as new, by the Arctic Health Research Center laboratory, from the peculiar habits of the long-lived females of a captive colony, the first such colony of northern mos-

quitoes to be established (1). It was designated the *C. impatiens* type when single broodedness and obligatory hibernation of the female, a new combination, were proved. No temperate or tropical mosquito biologies like this have been described.

Some authors have observed the nonbiting habit of first-season females, others the viciousness of second-season hibernators of this species, and as a result the literature is cluttered with contradictory appraisals of *C. impatiens* as a pest.

It was soon obvious, from otherwise puzzling field data, that *Culiseta alaskaensis*, as well as the local *Anopheles* and *Culex*, shares the new type of life cycle (2). In this cycle the habits of females are sharply divided between the two summers they live. Courtship and mating take place the first summer, engorgement and oviposition the second. An adult *C. impatiens* female survives 10 or 12 months. After mating, the females find shelter for diapause. This rest period of estivation and hibernation lasts as long as 10 months in nature; it is as brief as $3\frac{1}{2}$ or 4 months in the laboratory colony where it ends abruptly with many females spontaneously rousing to seek blood.

Normally, the blood lust appears concomitantly with increasing light in early spring, and the hibernators will bite at near freezing temperatures in order to develop and lay the egg rafts about 2 weeks later. The comparable preoviposition period of *C. alaskaensis*, however, averages much longer, 32.1 days. In both instances the preoviposition periods are unprecedentedly extended as contrasted with those of temperate zone mosquitoes. *Culiseta inornata* of the northern United States requires only 5.3 days (3). Many tropical *Anopheles* actually engorge, develop, and lay eggs all within a 24-hour period.

The preoviposition periods of *C. impatiens* and *C. alaskaensis* were not curtailed under experimental conditions at temperatures above 20° C. Such abnormal warmth merely caused excessive mortality. Eggs, larvae, and pupae of forms subject to the *C. impatiens* cycle develop without diapause in relatively warm permanent or semipermanent waters.

Another cycle characteristic of all Alaskan northern Aedes was made known by Wesenberg-

Lund of Denmark 35 years ago (4). He designated it the A. cinereus cycle. Hibernation takes place in the egg, and all the forms are obligatorily single brooded. Larvae, and sometimes the pupae, tolerate cold well. Aedes communis, for instance, can develop normally in water as cold as 2°-3° C. Females of this type mate, engorge, and oviposit within a few weeks after emergence in May or June. Eggs are laid in drying basins of vernal pools or along the dried margins of less transient standing waters.

Cold Resistance

Pronounced cold resistance characterizes winter and spring stages of northern mosquitoes, namely, the eggs of Aedes and the adult females of other genera. At these stages the pests withstand months of heavy frost and the fluctuating temperatures of spring breakup. Activities of the adult hibernators are also surprisingly independent of moderate cold above freezing. C. impatiens females have been observed in January and February frisking on the wing and resting on the snow.

However, specific differences of degree of cold tolerance significantly distinguish the less adapted stages in both cycles. The score or so of Aedes can be arranged naturally in serial order based on water temperatures typical for a critical advance in stage: (a) temperatures at which the eggs hatch; (b) temperatures characteristic of mass pupation; (c) the seasonal order of appearance of the species on the wing. Whether the criteria used be (a), (b), or (c), the resulting arrangement is practically the same. Larvae of the earliest species may precede the latest in subarctic Alaska by 2 months (5). Thus the observer dips the former from bleak snow-melt pools after cracking the ice cover of the preceding night, whereas he encounters the latter during the bright, warm days of lush new foliage in early summer.

However, surveys which classify mosquito species according to breeding area, region, and elevation rather than by collection data are particularly instructive. Lumped records for a given species from different habitats may be deceptive where there is thermal individuality dependent on size, exposure, source, and depth of breeding waters as well as their altitude and latitude. Unexpected contrasts in optimal temperature ranges sometimes isolate the most closely related species. For example, A. communis, one of the earliest larvae thriving in the lowest temperature range is nevertheless close taxonomically to Aedes pionips, a late warmwater larva. Larvae of all forms manifesting the C. impatiens cycle presumably never tolerate cold as well as any of the Aedes, and larval cold tolerance is thus closely bound up with life cycle type. Cold tolerance and cycle type are not only implicated in larval habitat preference, but also in geographic distribution (6).

Distribution

Geographers define arctic, subarctic, and temperate regions by physical criteria stressing winter cold and latitude, such as January isotherms and distribution of permafrost. To explain insect distribution in Alaska, zoogeographers must emphasize vegetation types and warmth during the all-important summer. Otherwise the terms arctic, subarctic, and temperate have practically no meaning.

The Territory is mountainous, and alpine arctic islands above the low timberline at 1,500–2,000 feet are strewn helter-skelter over temperate and subarctic regions. Moreover, without regard to elevation, there are vast remnant glaciers of the Pleistocene ice sheets which chill "temperate" southeastern Alaska. (These ice sheets never covered the arctic and melted in most of the subarctic at the time they receded from the northern United States about 5,000 years ago.)

For example, although southeastern Alaska is designated "temperate" because of the mild winter climate, its cool summers limit the fauna to hardy forms. In the warmer subarctic, where maximum summer temperatures are 90°–100° F., southerly species, such as sun-loving Anopheles occur. Finally, "arctic" treeless tundra extends far into the subarctic in western Alaska and merges with the Aleutian grasslands at the latitude of temperate southeastern Alaska.

In the arctic there are wooded valleys of spruce, willow, and birch representing to the biologist simply subarctic inclusions comparable to the arctic alpine inclusions. In fact,

the "hemiarctic" zone proposed by Rousseau, which means demarcation between arctic and subarctic, may constitute a broad band of transitional parkland (7).

Trees are an important part of the environment to mosquitoes. Culicidologists conveniently designate forest forms "woods" mosquitoes. Species of open country are "tundra" or "prairie" mosquitoes. There is a sound ecologic basis for the practice. As more is learned about the distribution of northern mosquitoes in forest or treeless areas, apparent contradictions are resolved. It is essential to stress local habitats and to soft-pedal climatic regions for progress in understanding distribu-Nevertheless, interesting contrasts of arctic, subarctic, and temperate lists of mosquitoes may be made with reference to their qualitative and quantitative compositions, biologies, seasonal histories, and the practical importance of some species as pests.

Arctic Fauna

Several excessively abundant so-called dark-legged species of *Aedes*, especially *communis* and tundra forms of the *punctor* complex, are the most important arctic mosquitoes (8, 9). When *Culiseta* occur at all there they are scarce and restricted to wooded valleys. *Culex* and *Anopheles* are absent, and any importance of the *C. impatiens* type of life cycle is academic in the arctic. For this reason, too, the mosquito-biting season lasts less than a month, even though at peak it is probably the most intense in the world.

Subarctic Fauna

The rich and varied subarctic mosquito fauna contains about 2 dozen species belonging to both of the northern types of single-brooded life cycles. The very large Culiseta pests of early spring are joined during May and June by 8 or 9 small dark-legged Aedes and later further reinforced and replaced by about as many, typically larger, banded-legged kinds. Two retiring and local Anopheles and Culex species at their northern limits emerge in midsummer. Over vast areas the mosquito-biting season extends from late April to early August, or nearly 4 months. Mosquito densities are high in the interior valleys and locally along the coast at

mouths of streams, causing severe pest problems in the flat areas most desirable for human habitation.

Temperate Fauna

The so-called temperate southeastern Alaskan mosquito fauna is rather similar to the subarctic list shortened to a dozen species (10). C. impatiens appears early (March) in hordes. C. alaskaensis occurs only as far south as Haines, the northern gateway to southeastern Alaska and the sole locality in the region for Culex. Anopheles is absent, too, so far as known. In compensation, two Californian species of Culiseta, incidens and maccrackenae, have entered from the south. Either species may pursue a temperate zone life cycle; be multibrooded or have larval hibernation. Unfortunately, both species are rare and their biologies uncertain in Alaska.

The mosquito-biting season in southeastern Alaska is approximately 5 months, but pest problems are markedly local and are almost always due to forms of the A. punctor complex, for example, Aedes punctodes, a salt marsh breeder. The dark-legged species with, of course, the A. cinereus cycle, thus so predominate that southeastern Alaskan mosquitoes, both taxonomically and biologically, resemble the arctic and subarctic faunas rather than typical temperate zone mosquito faunas.

Mosquitoes of all three life zones in Alaska are different from most stateside mosquitoes, but as they have a great deal in common, it seems logical that they be studied and controlled from a central headquarters in subarctic Alaska.

Larval Habitats

Definition of the typical larval habitats of insects harmful in adult stages facilitates further biological study and makes species sanitation feasible. As an extreme example, for many years Alaskan entomologists have been stymied in studies of the common snipefly pest, Symphoromyia atripes. They could not find its breeding places, immature stages, or the males. In 1955, however, the first newly hatched Alaskan Symphoromyia appeared in emergence traps put out in mountain meadows for sampling alpine insects. It is at long last reasonable

to anticipate progress in learning the biology and planning the suppression of snipeflies.

In the main, the most harmful Alaskan mosquitoes worthy of special suppression measures include A. punctor forms, communis, impiger, excrucians, fitchii, intrudens, diantaeus, and C. impatiens and C. alaskaensis. It is difficult to be objective quantitatively about culicine larval populations; the common forms are usually listed for the sake of completeness from a wide variety of marginal atypical habitats. However, only favorable habitats, where a species is so abundant as to cause concern, ought to be considered typical. By reasoning so, at any rate, it has been possible for entomologists to characterize the habitat of each Alaskan mosquito, for all practical purposes. Several representative examples of Alaskan mosquito habitats have been described in detail elsewhere (11-13).

Quaking Bogs

Public Health Service entomologists have shown that *Drepanocladus-Carex* quaking bogs are the preferred larval habitat of only one Alaskan *Aedes* (11). In his northern Michigan sphagnum mat-mosquito study, Irwin (12) reported a perplexing wiggler resembling *A. diantaeus*. The new species was described by Smith (13), who discovered it in a Massachusetts quaking bog, and named *Aedes pseudodiantaeus* (now called *Aedes decticus*). It is now practicable to study the biology of *A. decticus* where it abounds in Alaskan quaking bogs.

Permanent and Semipermanent Waters

The characteristic mosquitoes of weedy lakeshores and permanent ponds in Alaska are Anopheles and Culex. Their specific environmental requirements differ markedly, nevertheless. The sun-loving Anopheles occurs in the open, and especially in warmer water than the shade-loving Culex which hides in clumps of Carex and other sedges.

Dystrophic ponds within bogs are the preferred habitat of *C. impatiens* and *C. alaskaensis*. However, the *C. impatiens* female deposits her raft freely on the open water of weedless basins whereas *C. alaskaensis* oviposits chiefly within dense clumps of dead *Carex*. Consequently it is feasible to predict, in regions where

both species occur, which larva will predominate in a particular pond. Culiseta morsitans also breeds in pondlike bog inclusions but primarily in senescent bogs of the Sphagnum-Ledum-Picea class which are choked with Myrica gale or Carex.

Tundras

In the boggy pools of the vast arctic and subarctic tundra waterscapes, there develop distinct tundra varieties of two species of the A. punctor complex. Whatever the taxonomic category to which these perplexing varieties are assigned, they certainly constitute major pests. It was recently shown (14) that the A. communis form, breeding in the brushy inclusions of the tundra and alpine meadows, manifests habits not typical of the species. The males are able to swarm for mating in the open treeless wastes even though A. communis is typically a "woods" mosquito swarming only in deep shade. Possibly this open-country form should be considered a tundra variety of A. communis.

Salt Marshes

Alaska has an important salt marsh mosquito pest which belongs to the A. punctor complex like the principal tundra pests. It breeds in myriads in arctic, subarctic, and temperate brackish coastal marshes. Dyar designated this form A. punctodes, and it may be necessary to restore its specific standing when the puzzling A. punctor complex becomes better understood. At any rate, the basic knowledge of its biology for settling academic questions and undertaking practical control of salt marsh mosquitoes is now being acquired (15).

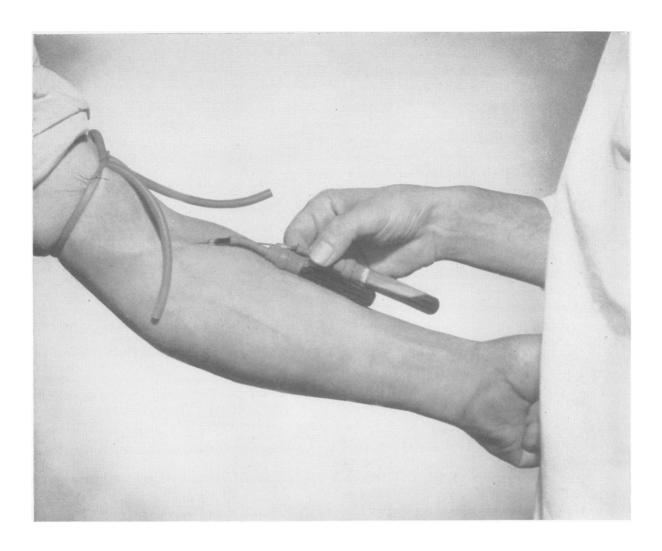
Summary

Certain general correlations of life cycle with cold-tolerant stages and geographic distribution of mosquitoes in Alaska have been noted. Similarly, there is correlation of habitats with type of cycle. The species belonging to the Aedes cinereus cycle breed in temporary waters or the drying margins of semipermanent waters. The earlier species develop in snow water retained by the underlying frost. The later species require water which persists longer. Species of the Culiseta impatiens cycle, however, occur only in permanent waters or the most persistent

residual pools of semipermanent waters. There are no Alaskan species known to breed normally either in artificial containers such as tin cans or in treeholes, the water of pitcher plants, or other small collections of water.

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idea

Piggyback Blood Testing

The Sheppard vacuum-packed blood-testing tube has been used in mass blood-testing programs by many State, county, and city venereal disease programs for the past 5 to 7 years.

The Sheppard tube proved to be a valuable aid to the speed and efficacy of mass blood testing. Occasionally, however, a tube with a faulty vacuum would fail to draw blood, necessitating a second attempt.

Survey workers using the tubes readily developed the technique of

leaving the first needle in the vein and inserting the needle of a second tube into the rubber sleeve of the first, releasing the vacuum and drawing blood into the second tube via the first tube, thereby avoiding a second venipuncture.

The picture above, taken by Dr. Charles M. Cameron, Jr., of the University of North Carolina School of Public Health, shows blood specimens being taken in this manner during the Cherokee Indian Reservation multiphasic survey conducted by the North Carolina State Board of Health in April 1955.

As a result of this experience in the piggyback method of blood drawing, the District of Columbia Department of Public Health has combined both syphilis and diabetes detection in a mass blood-testing program.

Prepacking the second tube with 30 milligrams of sodium fluoride is the only special preparation required for the dual testing. The sodium fluoride acts as a sufficient anticoagulant for 3 cubic centimeters of blood and allows refrigeration storage of the specimen until it reaches the laboratory.

The piggyback blood-testing method was introduced in Washington, D. C., in June 1955 in a house-to-house blood-testing survey. The reaction of the public was, "Two tests for the pain of one is only half bad."

—John L. Pendleton, U. S. public health representative District of Columbia, Department of Public Health.