

BIOLOGY OF AN ALASKAN MOSQUITO, *CULISETA ALASKAENSIS* (LUDL.)

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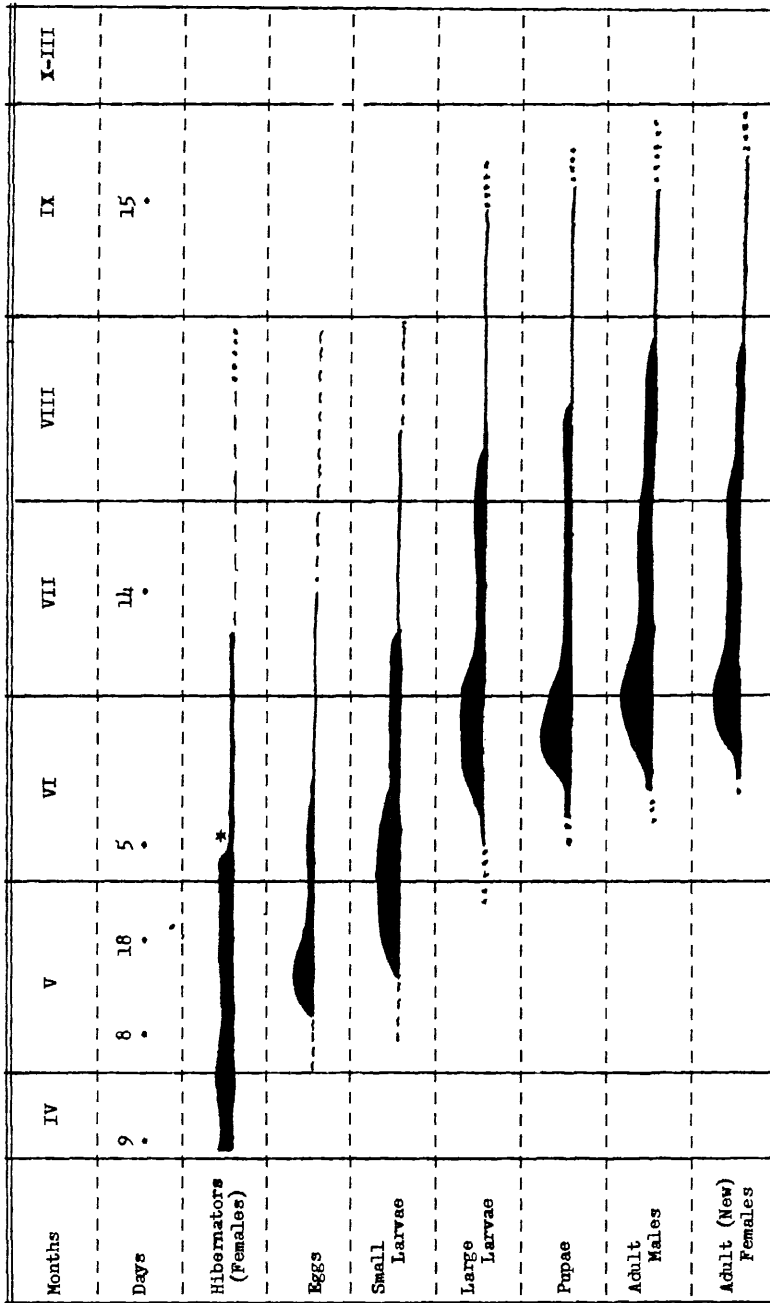
In a recent study of *Culiseta impatiens* (Wlk.) the stages of *C. alaskaensis* were frequently encountered (Frohne, 1953). In fact, the two species have similar biologies and often occur in the same habitats in the Upper Cook Inlet region, Alaska. Their life histories differ fundamentally from those recognized for temperate zone mosquitoes, resembling most the *Culex pipiens* type of life cycle (Bates, 1949). Recognizing that the differences from that well known cycle are fundamental, and believing them to be shared by at least one subarctic species each of two other culicid genera, a new life-history type, the *Culiseta impatiens* type of life cycle, was proposed for all such subarctic mosquitoes in a previous paper (Frohne, 1953). The essential common characteristics in biologies of this type are obviously adaptations to the far northern climate. There is one brood annually, the females of which mate the first summer. Then, so far as is known, they invariably enter a very long diapause, oviposit during the following summer and die at last about a year after emerging from the pupa. This sex is thus obligatorily biennial whether the individual females emerge in June, midsummer, or not until September. A striking phenomenon during the spring breakup of many northern regions is the sudden appearance of hordes of the large and vicious hibernators (females of certain species with this type of life cycle) which are seeking blood even before the snow cover has melted.

Culiseta alaskaensis is a holarctic species, peculiar to wooded, subarctic regions primarily, with incursions in small numbers into colder, especially mountainous, regions to the southward. In North America it ranges across Canada from British Columbia to the province of Quebec (Jenkins & Knight, 1952) and southward into some of the Rocky Mountain states. In the Old World it is known from Northern, Northeastern, and Alpine Central Europe; and from Siberia and the Caucasus Mountains in Asia. Over most of this vast range it is reportedly an uncommon species; for example, Rempel (1950) for western Canada says "it does not appear to be common in any area," and Natvig (1948) in 21 years' collecting found only two Norwegian larvae. In Alaska, however, the species is common or abundant apparently over much of the Interior south of the Brooks Range and along the Pacific Coast at least from the mouth of the Yukon River (Berg, 1951) southward to Haines.

METHODS

The field and laboratory data on *alaskaensis* were obtained as described in the previous paper on *impatiens*, (Frohne, 1953) to which reference will be made repeatedly in this paper without reiteration of

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* Hibernating and aestivating females are ignored.

GRAPH I. Annual cycle of *C. alaskaensis* at Anchorage, Alaska (1950-1951 data).

the source. Unfortunately, it has not yet been possible to induce mating and to colonize *alaskaensis*. However, rafts were obtained in the laboratory and the periods, including engorgement to oviposition, longevity of hibernators, etc., were studied with captive hibernators in small, screened cages. When the microhabitat for mass oviposition was found, spot characters for identifying *alaskaensis* rafts were soon worked out. Thus in 1951 it was practicable to hatch and rear the species in quantity from wild eggs. Larval rearing technics successfully used with *impatiens* worked nearly as well for *alaskaensis*. The adults secured in this way were not robust, however, and ordinarily did not copulate. Ponds with *alaskaensis* in pure culture and at high density were sought fruitlessly for two years in the Upper Cook Inlet. Meanwhile the separation of *alaskaensis* from *impatiens* larvae was found to be tedious. Errors were also made which could not always be corrected easily later on, especially as some of the adult males of *alaskaensis* had inconspicuous or no tarsal rings. Recourse was finally made to collection of large larvae and pupae at Mile 172 (from Anchorage) Glennallen Highway where about 6,000 large *alaskaensis* larvae and pupae were netted with the screen-bottom bucket. Data on prevalence and dispersal of the hibernators are based on 1950 landing rates (Frohne, 1951) and on light and fan trap collections of May and June, 1951, which proved that this stage of *alaskaensis* not only disperses widely on the ground level but also occasionally flies as high as 100 feet. (Collections were made from the Civil Aeronautics Administration towers at the 100 foot elevation.)

Identification of large larvae and adults was aided by the published keys (Matheson, 1929; Natvig, 1948; Rempel, 1950), but none of them was entirely satisfactory for separating local *alaskaensis* and *impatiens*. Rempel proved most useful though the *alaskaensis* larva he figures has similar upper and lower head hairs. Alaskan material has upper head hairs similar among themselves but contrasting with one or two much larger hairs of the lower tuft. *Culiseta* larvae with one or two larger lower head hairs invariably produced *alaskaensis* adults in this study. The form of the species described by Rempel may also exist in Alaska. Larvae of this description ("head hairs short, multiple; upper head hairs with 7-10 branches, lower head hairs with 3-5 branches") occasionally appeared among normal *impatiens* larvae reared from known *impatiens* rafts. Adult females were easily separated by the wide, white tarsal rings of *alaskaensis*; but these rings are sometimes reduced to a few scales or are entirely absent in male *alaskaensis* which can, however, be easily distinguished by the spines of the 8th segment; few in *alaskaensis*, many in *impatiens*.

SEASONAL HISTORY

The annual cycle of *alaskaensis* in the Anchorage area is remarkably uniform from year to year. However, the variable growth rates found in laboratory rearing occur in nature also, so that it is better to speak of a preponderance of stage rather than a sequence of stages, except for winter and spring. The periodicity is characterized by: (1) the punctual appearance April 9-15 of the hibernators; (2) oviposition *en masse* in sheltered "nests" formed by entangled dead *Carex* plants May 8-18; (3) a succeeding period of 5 to 6 weeks of increasing

divergence of larval sizes until, from the middle of June to the middle of July, there is a chaos of stages, *viz.*, late eggs, larval instars, pupae, females of both the current and the preceding summer, and males; (4) disappearance of hibernators and new rafts in late July and early August; (5) disappearance of small larvae in early September; and (6) disappearance of large larvae and presently of pupae; then finally (7) disappearance of adults after mid-September. The preponderant immature stage at a given date may be determined by using graph I and table I together.

TABLE I
SCHEDULE OF STAGES, *C. alaskaensis*

<i>Event</i>	<i>Days after oviposition</i>
Raft Laid.....	0
Hatching.....	5
Molt to Second Instar.....	12
Molt to Third Instar.....	18
Molt to Fourth Instar.....	23
Molt to Pupa.....	32
Adults Emerging.....	37

It has not yet been positively proved for *alaskaensis*, as it was for *impatiens* that the female is obliged to hibernate or to undergo a diapause of several months before she can engorge and develop ova, but there is little doubt that this rest period is obligatory. The hordes of hibernators seen in April undoubtedly represent a considerable part of the annual generation of that sex. The vast majority of the new adults emerge in a peak about the last week of June. Assuming that those females which emerge during June and July do not simply die without reproducing, they would be expected to deposit rafts about August 1-15, having engorged several weeks earlier. However, there is certainly no increase of biting in early July or of rafts in August. On the contrary, biting decreases steadily during May and June (Frohne, 1951), so that July rafts like July bites are scarce and an August raft or bite is great rarity.

The laboratory observations that the females entered a diapause for three months (until October 14) before awakening to engorge within a few days, though suggestive, are inconclusive because no laboratory female was known to have mated and none oviposited in 1951. Unless virgin *alaskaensis* in diapause are awakened and stimulated to engorge by other causes than are normal inseminated females, the facts observed are in conformity with the thesis that *alaskaensis* will not engorge before a diapause lasting several months or more. A single laboratory-reared female did, however, lay a raft in November, 1950, many eggs of which were successfully reared for checking the identification. It is concluded that females of *alaskaensis*, like *impatiens*, undergo an obligatory diapause of about nine months which includes a period of aestivation for most of the sex which emerge in summer. This period is limited to about seven months hibernation for late females emerging in the fall.

When the quantitative data on rafts are considered, minor specific differences between the periodicities of *alaskaensis* and *impatiens* in the Upper Cook Inlet are evident, *e.g.*, that *alaskaensis* engorges first and oviposits about two weeks earlier. Most of this advantage, if such it be, is lost however, because *alaskaensis* has the longer average larval period by about nine days. It is not improbable that these differences relate to the occurrence of this species inland at higher elevations where *impatiens* is virtually absent.

HABITS OF ADULTS

The diverse observations of adult behavior may be summarized under: (1) Activities of males and young females, *i.e.*, Courtship and Mating and Feeding on Sugar Solutions; (2) Diapause, which has been noted under Seasonal History; and (3) Activities of Hibernators. Adults of different ages react to the same environmental stimuli, *e.g.*, changes in illumination. While the actual behavior of adults so activated is characteristic of the sex and age, there are also some common activities like feeding on the sugar sops and attempting to get through the screen of the cage. The diapause (age) completely separates the young females with mating instinct but lacking the blood-lust, from the old hibernators with their bloodsucking and ovipositing habits.

Courtship and Mating.

Efforts to establish a self-perpetuating colony of *alaskaensis* in 1950 and 1951 failed when the species did not copulate in screened cages. Only one laboratory-reared female has oviposited. This individual produced fertile eggs in December 1950 in the open insectary and presumably mated there. Dr. R. I. Sailer (personal communication, 1951) saw hovering of the males in swarms near Fairbanks, Alaska. Nothing like this has yet been observed in the present investigation.

Nevertheless, courtship behavior similar to the preamble to copulation in *impatiens* was frequently observed in brightly lighted small cages which had either been held for several hours previously in weak light or kept dark. In July, 1951, over a period of about three weeks, comparative observations of courtship in *Culiseta alaskaensis*, *impatiens*, and *morsitans* were made which probably indicate the relative degree of stenogamy of each. The numbers of adults were about 4,000, 20,000, and 900 respectively, but the densities in the individual foot-square cages were usually much the same. There was no courtship activity in *morsitans*, though general activity, including feeding on sugar sops, was as great as for the other two species. *Impatiens* courtship, which was occasionally followed by copulation, was similar to and no more impetuous than the behavior of *alaskaensis*. But the *alaskaensis* males did not manifest clasping reactions or copulate in any of scores of courtships observed.

In courtship the male *alaskaensis* crawled or flew to a female, followed her if she flew off, grappled at her thorax (venter) with his enlarged prothoracic claws and sometimes attached himself there. None was seen to manifest grappling reactions with the terminalia, and after half a minute or less the mating urge apparently weakened and he let go and left her. Thereafter he rested or tried to escape at the top of the cage.

Diapause

Diapause is used here to indicate a long period of inactivity of the female which occupies most of the first summer ordinarily and all the succeeding winter of her life. Practically nothing has been learned about this compound aestivation-hibernation in *alaskaensis* to show whether or not it is a deep uninterrupted lethargy and what its location may be. But it is necessary (*v.s.*) to postulate the diapause as the simplest, most probable explanation for the peculiar periodicity of the females in nature and for their behavior in the laboratory. In captivity young females were active only about two weeks while the males were present and attentive. Thereafter females squatted close against the cage screen or frame in a stance quite like that of hibernating *Culex pipiens*. If prodded they reluctantly shifted and if made uncomfortable with a hot light bulb they took flight. Similarly they could be forced to change position in the cage by allowing all but one corner of the humidity towel to dry up. In 1951 eight probably virgin survivors, after about 95 days at room temperature, resumed activity and engorged but none lived to oviposit. It is noteworthy that presumably inseminated *impatiens* awakened and engorged the same week and similarly perished without ovipositing. In November of the preceding year when laboratory colonized *impatiens* laid many rafts, an *alaskaensis*, survivor of some reared pupae inadvertently misplaced in the *impatiens* cage, also oviposited. It had evidently actually mated and gone through its diapause in the insectary cage. The raft laid by this female was also reared; the progeny were *alaskaensis*.

Feeding

Sugar Solution. Both sexes sucked sugar sops, beginning about three days after emergence and fed intermittently on them until death (laboratory). Females in diapause were occasionally seen taking sugar suggesting that aestivation in warm weather may differ greatly in degree of lethargy from hibernation. Slices of oranges or apples were preferred to the cane sugar solution.

Blood Sucking. The habit is believed to be restricted to hibernators in nature. In the laboratory only eight females which survived about 95 days awakened and engorged successfully; others died with or without attempting to bite after resumption of activities in mid-October 1951. Although opportunity had been offered these females on alternate days for a month previous to awakening none bit until all eight did the same three days chosen by most of the *impatiens* which were handled similarly and also behaved similarly. Since these mosquitoes of both species died without ovipositing and were not dissected, it is uncertain whether they had mated. The quantitative field data like the laboratory observations indicate that the young females do not bite their first summer and that the steady decrease in biting and in the number of new rafts in the field during May and June corresponds to the cumulative mortality of the hibernators.

The factors stimulating biting are probably complex. In the early spring *alaskaensis* prefers to bite in the bright sunshine. The survivors of late spring and summer, however, are apparently less avid and are chiefly twilight and in-the-dark biters. The wide range of air tempe-

ratures at the ground over which biting was observed in nature, (41° - 70° F.), or the probable optimal biting temperature range of 55° - 65° F. as determined roughly in the laboratory, suggest that warmth is seldom the decisive determining factor for biting. Nevertheless, the landing rates over a period of a week of increasingly warmer weather in spring were observed to rise consistently (Frohne, 1951) even though the actual population on the wing, unfed, was presumably decreasing. The preference for biting at rather low temperatures, however, may explain in part the shift to night biting in summer. Interesting specific differences in biting rates were noted in areas where large populations of *alaskaensis* and *impatiens* hibernators occurred together. At Rabbit Creek collections were made daily in good weather for two weeks in late April and early May which showed: (1) *alaskaensis* bites earlier in the spring; (2) there are *alaskaensis* days when it bites almost alone, and also *impatiens* days when few *alaskaensis* are seen; (3) most commonly both species bite simultaneously, the proportion of either varying from day to day or even from hour to hour; (4) the locus of biting in a small, hilly, wilderness area of about 10 acres also gave a different percentage of species according to place, e.g. a large and dense *Culiseta* population was about 90% *alaskaensis* on a gusty, exposed hill top whereas a much smaller population in the sheltered valley at its foot 150 feet below was approximately 75% *impatiens*. Thus the factors influencing biting seem to differ slightly in kind or degree for the two species of *Culiseta*.

The observations on biting relate chiefly to wild hibernators held captive in the laboratory. They could usually be persuaded to engorge once during the week after capture, if not immediately, then by stimulating them with bright light and/or the breath. One in three or four would reengorge about three and a half weeks later, usually without having oviposited. At approximately 65° F., nineteen were timed on different occasions from the instant of inserting the mouthparts to their withdrawal when the insect invariably flies heavily away. The biting period of these captives ranged from 2.5 to 11 minutes, averaging 5.7 minutes. The forehead is a preferred biting site in the laboratory as in nature, but those landing elsewhere on the skin usually bite without much preliminary probing or moving about. *Alaskaensis*, a very large mosquito, is a painful biter and it frequently attacks close to sensitive organs, especially the eyes. With *impatiens*, *alaskaensis* entered houses and places of business in Anchorage in May 1950, and the city resorted to a truck equipped with an aerosol dispenser of DDT.

Oviposition

The eggs are laid in characteristic rafts by the hibernators following engorgement. This was studied with wild hibernators caged in individual lots which had engorged the same day. The period between engorgement and oviposition so determined is highly variable and sometimes exceedingly long. Frequency Table II of 53 ovipositions of 1951 indicates a range of 7 to 53 days and an average of 32.1 days. The contrast of this subarctic mosquito with certain tropical *Anopheles* which oviposit the day after engorgement is noteworthy. It is likely that the two rafts laid sooner than 15 days after engorgement in the laboratory belonged to females which had had an earlier blood meal in

the wild. It was established that some hibernators would take an additional blood meal before ovipositing.

The long lapse after obtaining blood before laying might be due to slow digestion of the blood at low temperature, but the seasonal data indicate that higher temperatures do not shorten this period. In fact, the 21 rafts of the frequency series which were laid in May (when most rafts are laid in nature) were produced an average of 21.7 days after engorgement whereas the 32 June-July rafts were laid an average of 38.9 days after engorgement. Even in the laboratory May was cooler than June.

TABLE II
THE NUMBER OF DAYS AFTER A BLOOD MEAL WHEN CAPTIVE
C. alaskaensis HIBERNATORS OVIPOSITED

<i>Number of Days</i>	<i>Number of Rafts</i>
10-14.....	2
15-19.....	7
20-24.....	5
25-29.....	7
30-34.....	9
35-39.....	9
40-44.....	6
45-49.....	5
50-54.....	3

Two other factors appeared to have had more influence than low temperature in extending this period in the laboratory: (1) unwillingness to oviposit in cages, for a majority of the blooded hibernators died without ovipositing although dissection showed the eggs had developed and there were viable spermatozoa in the spermathecae; (2) age, since the captive females requiring the longest period to lay after the blood meal were also the oldest mosquitoes. (The three instances exceeding 50 days were among the last five rafts). Fortunately in this instance field data are helpful for it is certain that the earliest mass biting occurred about 31 days before the earliest mass oviposition.

Impatiens hibernators caged side by side with *alaskaensis* were almost equally reluctant to lay in captivity, so that a majority died without ovipositing and yet most of the layers did so in 14 to 15 days and none more than 35 days after engorgement. It is thought likely therefore, that *alaskaensis* actually requires 1.5 to 2 times as long (21-30 days) to develop the eggs as *impatiens*.

Finger bowls containing pond water with soil added were evidently not satisfactory for oviposition, or possibly more space is desirable than the foot-square cages provide. In May, 1950, veritable flotillas of *Culiseta* rafts were collected from within the shade of certain dense clumps of dead *Carex*. When it was learned a year later that these were *alaskaensis*, further observations were made showing that almost all the rafts of this species in a particular pond are laid in a few clumps of sedge which can be pointed out by a practiced observer without actually seeing a single raft. In the small pockets arched over by the

enclosing emergent dead growth of the previous season, the rafts are often arranged in attractive rosettes formed of 4 to 12 separate rafts ordinarily each with the pointed end directed inwards. For this reason bunches of dead *Carex* culms and leaves were placed in the oviposition bowls in cages with gravid females in an unsuccessful attempt to stimulate laying of caged hibernators. However, no more rafts were laid in bowls with the clumps than in others without them.

Longevity

In the laboratory. Adults of both sexes of *C. alaskaensis* live relatively longer than most mosquitoes. The life span of the male in the laboratory was commonly two to three weeks for reared material. The oldest individual male lived 44 days. The laboratory longevity data for females are incomplete, *i.e.* much too short because dated females were not held over winter. Even those which came out of diapause in mid-October to engorge, died before it was time to oviposit. About 50 of these died at 15 weeks or less (of adult age). To oviposit once they should have lived about two weeks longer. Hibernators captured in nature in April and May lived one to three months in cages. They generally engorged after capture and about 20% laid, usually immediately before death. The oldest individuals presumably were those which lived until midsummer; the last one died July 20. It is thought probable some of these hibernators had reached a year of age as adults.

In Nature. Graph I, the annual cycle of *alaskaensis*, summarizes the longevity based on field observations. The peak pupal emergence period of females in 1950 came in the final week of June. The following spring the hibernators were abundant until about the last week of May. These data indicate a female longevity of 10 to 12 months. The percentage which survives this long and oviposits is conjectural. The August larval collections do not support considering emergences later than July, which are relatively few, as comprising any considerable part of the annual production. If July emergences are assumed (without basis) to survive better than the heavier June emergences, the July females would still be about ten months old the following May at peak oviposition time. On the other hand, the scattering stragglers, hibernators which engorge and oviposit in July and rarely even in August, are possibly 13 to 14 months old. (The reasons for discounting the possibility that *alaskaensis* might engorge and oviposit the summer they emerge are evident, too, in Graph I and they will be reviewed in the Discussion.)

AQUATIC STAGES

Habitats

Like *Culiseta impatiens*, with which it is usually associated in the Upper Cook Inlet breeding ponds, *alaskaensis* occurs in diverse aquatic habitats. These may be very generally characterized as *permanent or long-standing lenitic waters*. Excepting some differences in the distribution of the larvae, which will be noted presently and which are chiefly quantitative, the description of the larval habitats of *impatiens* in the previous paper is applicable to *alaskaensis*. Mosquito larval distribution, as has been observed by malariologists, is largely determined by

the ovipositing female. This is the case with *C. alaskaensis* and *impatiens*. The *alaskaensis* habit of laying the eggs in the shelter of plants, especially of dead *Carex*, is obviously related to predominance of that species in *Carex* marshes and to its uncommon occurrence in all open, man-made excavations where vegetation is scanty or absent and where *impatiens* larvae may literally teem. In the region studied the fresh-water marshes and bogs almost invariably provide satisfactory egg-laying microhabitats for both species. Determination of the species composition was done by dipping during the latter half of June and in July, since May counts favored *alaskaensis*, August counts *impatiens*. *Culiseta morsitans* was sometimes present as well as its two congeners, even predominating in certain ancient *Myrica*-sphagnum coastal bogs, a type of larval habitat overlooked by Jenkins (1948) which is of minor importance for *alaskaensis* or *impatiens* but produces nearly all the *morsitans* in the Upper Cook Inlet region.

The larval distribution in varied fresh waters with from little to much organic matter suggests that organic pollution would probably be tolerated by *alaskaensis* but that salinity would not be. The particular pond from which the wild larvae were collected in quantity was foul-smelling and almost colorless. Many others, especially bogs and *Carex* marshes, were tea-colored with colloidal organic acids. As to saline larval habitats, rafts were occasionally collected from the freshest fringes of salt marshes in the spring. In late July these were flooded with Cook Inlet water (1,000 parts free chlorine per 100,000 or 50% of sea water). No larvae were dipped from such salt water, however, and the earlier rafts had been laid in snow-melt water with only 10 parts chlorine per 100,000. Furthermore, after flooding, rapacious throngs of the stickleback, *Gasterosteus aculeatus* L., and its fry dominated the same areas. Actually no *Culiseta* larvae of any kind have been collected in this study in water more saline than 25 p.p.h.t.

Organic Pollution. In the laboratory rearing data also suggested a high degree of tolerance for organic pollution by all aquatic stages except the newly hatched larvae. A proportion of second stage or older larvae placed in foul water consistently survived to pupate provided heavy films or low surface tension did not interfere too much with their reaching the air. In foul pond water, which was added to but not changed during 30 days, a few surviving first stage larvae grew to the third stage. Since changing the water every few days so as to keep it fresh increased survival greatly but still did not produce robust adults as a rule, it was tentatively concluded that the rearing technic was unsatisfactory in some way not directly related to pollution, fouling, or high organic content of the water.

Salinity Tolerance. Salinity tolerance was also tested in a preliminary way with larvae of various stages in the laboratory. Pond water was salinified with Upper Cook Inlet water which was titrated for chloride with silver nitrate after adding test larvae. The initial salinities increased by evaporation so that a terminal titration (in parentheses in the following series) was necessary: 20(22); 32(49); 37(40); 51(70); 68(96); 70(87); 85(120); 210(390); 300(440); 412(630); 500(790); p.p.h.t. Up to about 70 p.p.h.t. there was partial survival for more than 96 hours of second and third stage larvae, but the first

and fourth stage died out entirely within 24-48 hours. No stage molted successfully in water more salt than 50 p.p.h.t. (In contrast, *Aedes impiger* (Wlk.) and *punctor* (Kirby) larvae and also pupae molted and the larvae grew with increasing mortalities in the same vessels with salinities up to about 500 p.p.h.t. or ten times as saline as that tolerated by *alaskaensis*. In the fresh-water controls the *Culiseta* larvae survived better than the *Aedes*.) There is no indication here that *alaskaensis* shares to any considerable degree the capacity of its close European relation, *C. annulata*, (Schrank), to breed in brackish waters.

Eggs and Rafts

The rafts of *alaskaensis* are apparently new to science although the general description of the rafts of *impatiens* in Howard, Dyar, and Knab (1915) tempt one to suppose an error was made in which an *alaskaensis* raft collected with *impatiens* larvae, was mistaken for *impatiens*. Probably *alaskaensis* rafts have been overlooked or not properly associated because of the hidden egg-laying microhabitat, the extended lapse between engorgement and oviposition, the reluctance of captive females to

TABLE III
FREQUENCY DISTRIBUTION OF NUMBER OF EGGS PER RAFT
IN 58 UNFRAGMENTED RAFTS LAID IN THE LABORATORY
BY CAPTIVE *C. alaskaensis* HIBERNATORS

<i>Number of Eggs</i>	<i>Number of Rafts</i>
75-99.....	1
100-124.....	9
125-149.....	9
150-174.....	9
175-199.....	6
200-224.....	10
225-249.....	4
250-274.....	8
275-299.....	1
300-325.....	1
Total.....	58

oviposit, or if they are reared to mate, the long obligatory diapause required by those which have mated before they will lay. In the region of this study *alaskaensis* rafts have only to be distinguished from *impatiens* which can be done with the diagnostic key in the *impatiens* paper. They should not be liable to confusion with the only other mosquito raft known to occur locally, viz., *Culex territans*, Wlk., the eggs of which are grey unicolor, sharp-pointed at the upper (posterior) end and without a frill near the lower (anterior) end.

Descriptions. The rafts of *alaskaensis* are large and show considerable spherical curvature, which raises the ends of an arrowhead or falling drop outline boatlike from the water. The eggs are conspicuously striped transversely, there being ordinarily three tan annular zones (stripes) between four dark-brown ones. Eggs are commonly several microns more than a millimeter long. Although the raft of *alaskaensis*

is much larger than the typical *impatiens* raft there is a good deal of size variation as shown by Table 3, the frequency distribution of number of eggs for 58 laboratory-laid rafts of 1951. The average number of eggs is 183, and it is believed that rafts with less than 100 eggs are invariably incomplete. The largest rafts, comprising over 300 eggs, were rare in the laboratory material but were not infrequently collected in the field in May. In the laboratory, rafts about as large as those of May were laid later in the season (June-July), although the egg-developmental period, or more precisely the time from engorgement to oviposition, was much longer later in the season.

Incubation and Hatching. Table I, the average periods in the immature stages indicates that hatching occurs about 4.5 days after oviposition. This is the incubation period at 60°-70°degrees F. which is probably in the optimum temperature range. This was determined from 71 rafts collected twice daily in the laboratory and hatched in individual dishes. A few rafts held at 45°-55° F. hatched in eight to nine days; some kept just above freezing died.

TABLE IV
FREQUENCY DISTRIBUTION, NUMBER OF DAYS OF LARVAL
LIFE, *C. alaskaensis* IN THE LABORATORY, 60°-70° F.

Days from Hatching	Number of Pupations
20-21.....	1
22-23.....	4
24-25.....	10
26-27.....	24
28-29.....	15
30-31.....	13
32-33.....	19
34-35.....	21
36-37.....	11
38-39.....	26
40-41.....	18
42-43.....	17
44-45.....	5
46-47.....	2

The hatching process is similar to that of *impatiens*. The eggs, which are laid creamy white, undergo a development of color and hardening differing chiefly in the appearance of the stripes in *alaskaensis*. The larvae burst into the water as the chorion ruptures a little above the frill. When hatching is imminent some or all of the eggs show the dark eye spots near the frill, and the egg stripes become blotchy. Newly hatched larvae, initially almost colorless, darkened at the abdominal saddles, the tips of the antennae, the head capsule, and the air tube within half an hour.

Larvae and Pupae

Instars and Stadia. Laboratory-reared and wild larvae occur in four instars separated by the head capsule widths, respectively 425, 650, 950 and 1450 microns. In practice, the first stage larvae are recognizable unmistakably by the egg tooth. Table I gives the average duration of each stage determined from insectary rafts reared separately. The day

stated for a given molt is believed to be the most representative. Excepting the first molt (to second instar) which actually took place mostly on the twelfth day as shown, the day given in the table however, is only the middle point for a period of a week or more during which individual larvae underwent the molt in question, though hatched the same day or even sibs from the same raft. The topic of growth, molts, and instars needs further investigation. It appeared probable, for instance, that certain larvae skipped the fourth instar. Pupation was the most variable as to time of all molts, *i.e.* the total days of larval life. This is well shown in Table IV illustrating the accumulative individuality in age attained by time of ecdysis to the pupa of some larvae reared at 60°-70° F. in a dark corner, which hatched the same day (May 16) in 1951. Disregarding the earliest and straggler pupations of these 10 pans, the pupal molt for comparable large numbers took place any time from 26 to 43 days after hatching (June 11-28). The shortest larval period was 17 days! Furthermore, about 20 larvae of the lot were discarded alive July 2, or 47 days after hatching. Nevertheless, despite this variability, the range given in frequency Table IV is characteristic not only of laboratory rearing but of the cycle in nature in May and June when a common beginning point makes direct observation practicable (*cf.* Graph I). There is about a month between the peaks of oviposition and pupation. This is the average larval period; the individual larvae seem to grow at just as variable rates in nature as in the laboratory.

The pupal period, 4 days for males and 5 for females on the average, was determined from twenty pupae of two lots, one of wild larvae, the other of non-robust laboratory larvae. In the same temperature range *impatiens* pupae averaged 2.5 and 3.5 days before emerging, depending on the sex. But one male *alaskaensis* emerged in 3.5 days while another took 8. More data might show that robust pupae typically emerge in less than 4 or 5 days. The male pupa which emerged after 8 days is noteworthy. Seguy (1950) considers the maximum normal pupal period for mosquitoes to be 5 days.

Habits of Larvae and Pupae. The activities of larvae and pupae of *alaskaensis*, like the habitats, are much the same as those of *impatiens*. The following observations, if not peculiar to *alaskaensis*, are characteristic of the species.

The first instar larvae disperse within two to three days after hatching, so that no concentration of them persists at the oviposition microhabitat. Unless the pond is little and the larvae abundant it is difficult to collect small larvae in quantity. In the laboratory crowding killed small larvae, *e.g.* hatches from isolated rafts left more than two to three days in half-pint jelly glasses suffered 50-90% mortalities. These larvae favor the shelter of vegetation and feed and rest chiefly at or near the surface rather than the bottom of the pond.

Larvae of third and fourth instar are somewhat gregarious or appear to be by choice of the same limited habitat. They gather in openings, especially the largest in the sedge stands. Experience with the screened bucket indicated that about one-third of their number is ordinarily visible hanging at the surface; the others are feeding and resting, or molting on the bottom. As the first moving shadow strikes the water the larvae at the surface also duck.

The pupae of *alaskaensis* average so much larger than *impatiens* that tentative field separations of species on size alone were almost invariably correct. Pupae concentrate within the sedges bordering openings where aggregations of large larvae occur. When young they are also found in the open, and there are markedly fugitive, and if frightened use the paddles to anchor themselves among debris on the bottom. About two days before emergence of the adult, white M-shaped patches of air appear under the chitin of the dorsum of the thorax behind the trumpets. These patches, which may blur to squares or ovals, seemed to be diagnostic for *alaskaensis*. At any rate they characterized pupae nearly ready to hatch, virtually blind and convenient for pipetting into emergence dishes.

DISCUSSION

The present pioneering study sketches the life cycle of *C. alaskaensis* in bold outline, leaving conjectural, however, the important adult microhabitats and the activities which take place there. Certain obvious adaptations to the subarctic, including: (1) single-broodedness; (2) the female an obligatory hibernator mating the first summer, engorging and ovipositing nearly a year later; are characteristic also of *C. impatiens*, *Anopheles occidentalis* D. & K., and in part of *Culex territans* Wlk. in the region of the study. A new type of mosquito life history called the *Culiseta impatiens* type of life cycle (*cf.* Bates, 1949, p. 44-46) was proposed in the previous study of that species. It is a curious reflection on the immaturity of northern mosquito studies that no detailed biological study of far-northern species of this type had appeared so far as known prior to the *Culiseta impatiens* paper, although Wesenberg-Lund had named the parallel northern type of life history, the *Aedes cinereus* type of life cycle, which is also single-brooded but hibernates in the egg. Thus the present biology of *C. alaskaensis* is of interest not only *per se*, but more especially as a second example of mosquito adaptation to the subarctic by conforming to this but lately recognized type of life cycle.

It is of interest to consider the origin of mosquitoes sharing this type of life cycle. We are indebted to Natvig (1948) for an extended consideration of the distribution of Fennoscandian mosquitoes, including *C. alaskaensis*. He concludes among other things that *alaskaensis* and *Culiseta bergrothi* (Edwards) are pristine subarctic species which probably survived north as well as south of the Eurasian Pleistocene glaciers and has named them "archiboreal species." In North America the distribution data for *impatiens* indicate it, too, like *alaskaensis*, is an ancient subarctic species. Other mosquitoes which have adapted to the north by assuming the *C. impatiens* type of life cycle have presumably invaded the subarctic more recently and in all probability, invariably have their centers of distribution in the north temperate zone where they are double or many-brooded. Among these immigrants from the south are some species of mosquitoes not well adapted to the subarctic which show apparently incipient stages of that adaptation in the coldest parts of their ranges. An especially interesting example is *Culiseta annulata*, a species which is many-brooded in southern Europe, North Africa, and Palestine, but which is supposed to be single-brooded in

Central Norway, double-brooded in Southwestern Norway. The single-brooded form cannot altogether qualify as exhibiting the *Culiseta impatiens* type of life cycle, however, because both sexes are reported to hibernate! It is reasonable to suppose that *Anopheles occidentalis* and *Culex territans*, when they have been thoroughly studied in Alaska will be properly described as "immigrants from the south." And *Culiseta incidens* (Thomson) in Southeastern Alaska which has not yet been studied there may either have acquired the typical *C. impatiens* type of life cycle, or be double-brooded, or even demonstrate hibernation of males like *annulata*.

A review of the evidence scattered through this paper indicating that the females of *alaskaensis* are actually obligatory hibernators was promised under Longevity. These data may be consulted in Graph I and the appropriate sections within the parentheses closing the following propositions: (1) Laboratory-hatched females did not engorge for about three months (Blood Sucking); (2) Biting reached a nadir in summer when mated young females became most numerous and it did not occur in fall (Seasonal History); (3) The amount of biting was usually roughly proportional to the estimated unfed population of surviving hibernators (Seasonal History, Blood Sucking); (4) Mass occurrence of rafts in nature followed mass biting by about 32 days, the determined average period for egg development (Oviposition, Table II); (5) The June peak numbers of large larvae was followed by a steady, uninterrupted decline (no later peak), and delayed larvae and late rafts of straggler hibernators adequately account for August-September larvae (Seasonal History, Instars and Stadia); (6) The field pupal data confirm the prevalence curve for the large larvae (Seasonal History, Table IV).

SUMMARY AND CONCLUSIONS

An account is given of the biology of *Culiseta alaskaensis* (Ludlow) observed in the Upper Cook Inlet region, Alaska and in the laboratory. The mosquito is single-brooded and the females are obligatory hibernators living about a year. They mate the first summer and engorge and oviposit the following spring. They exhibit the kind of subarctic mosquito life history which has been called the *Culiseta impatiens* type of life cycle in a previous paper. Habitats and activities of immatures and adults are discussed.

The serious pest problem caused by *alaskaensis* can be abated locally by adulticiding.

The effectiveness of larviciding a year in advance would depend on the species' flight range which is unknown. Economical control in regions with limited breeding areas might be achieved by a modicum of knapsack spraying in late May limited to a radius of a few yards adjacent to oviposition microhabitats.

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SOCIAL BEHAVIOUR IN ANIMALS, by N. TINBERGEN. Pp. xi+150, 67 figs. Methuen and Co., London, and John Wiley and Sons, New York, 1953. Price, \$2.50.

The approach and subject matter of this volume are somewhat different from what one would expect from its title. Insect societies and the behavior of animal aggregations such as herds, flocks, and schools are not considered as such; as the author points out, these subjects have been adequately covered elsewhere. The author attempts, rather, to deal with the underlying causes of social cooperation, a phase which has been largely neglected, or which has received misplaced emphasis along certain lines, for example, the peck order and transmission of food from one individual to another. Though he does not deny the basic importance of such ideas, the author feels that there are much more important factors, such as fighting within a species, the causation of threat and courtship behavior, and the function of "releasers" (that is, visual, auditory, or chemical signals which serve as stimuli for social reaction or coordination). Social behavior, thus conceived, means coordination between individuals, not necessarily in large groups, but in numbers as small as two or three.

This book has significance not only for the animal sociologist and ecologist, but for the student of other phases of animal biology as well. The systematist, for example, will find such passages as the following (p. 37) very meaningful: "This specificity [of courting behavior] is particularly needed in closely related species . . . the behaviour patterns of closely related species are always very similar, just as their morphological characters are. They simply have not had the time for wide evolutionary divergence. But in such species there is always some striking difference between mating patterns, at least if spatial (geographical or ecological) or temporal (differences in breeding season) separation does not render this unnecessary." Also, throughout most of the animal kingdom "signalling behaviour is innate" (p. 74) and behavior patterns and their releasers evolve, just as anatomical structures do. The teacher of entomology is often asked what value to the insect some of its bizarre structures may have. Perhaps the answer may often be found through the concept of the releaser.

Dr. Tinbergen has for many years been known as an authority in the field of animal sociology. His book makes interesting reading; its style is direct though not by any means monotonous, and it avoids all unnecessary technicalities. Though written with special reference to vertebrates, numerous examples are taken from the field of entomology. A thorough reading will well repay anyone interested in animal ecology, biology, sociology, systematics, or the general subject.—M. T. J.