EGG-LAYING HABITS OF MOSQUITOES IN THE HIGH ARCTIC[1]

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ABSTRACT. Oviposition behavior and oviposition-site preferences of the mosquitoes, *Aedes impiger* and *A. nigripes,* occurring near Lake Hazen, N.W.T. (81°49'N., 71°18'W.) are described. The first species oviposits in soil crevices, and the second on exposed surfaces of uneven texture. Both species lay eggs on pond margins only in warm moist sites that are sheltered from wind. Solar radiation, through its effect on ground-surface temperature and in conjunction with the slope and solar aspect of otherwise suitable sites, largely determines the location of eggs. The significance of the very clumped distribution of eggs that results from this fine adjustment of the response of ovipositing females to microclimatic factors is discussed.

INTRODUCTION

This paper presents a qualitative description of the oviposition habits of two species of mosquitoes, *Aedes (Ochlerotatus) impiger* (Walker) and *A. (O.) nigripes* (Zetterstedt) in the Hazen Camp area (81°49'N., 71°18'W.), northern Ellesmere Island, N.W.T. General features of this high-arctic site were reported by Savile (1964); the aquatic habitats there were described, and designated by numbers, by Oliver and Corbet (1966).

Both species lay eggs in July and August above the prevailing water level, in zones that are likely to be flooded at snow-melt the following spring. *Aedes nigripes* lays on exposed surfaces (Corbet 1965, 1966b) and *A. impiger* in crevices in the soil (Corbet 1966b). *A. nigripes,* at least, oviposits only when directly insolated; thus the distribution of eggs on surfaces of different solar aspect can yield information on the diel periodicity of oviposition (see Corbet 1965, 1966a, b).

In this paper our main intention is to document the behavior of females during oviposition and to describe some of the site preferences that result in an uneven spatial distribution of eggs around the habitats in which larvae and pupae occur. Such information may guide observers who wish to find eggs of these species in similar habitats.

METHODS

Observations of ovipositing females were made (by P.S.C.) during the summers of 1962, 1963 and 1966. The margins of most ponds in the Hazen Camp area were systematically searched for eggs from August 5–15, 1963, and examined as opportunity permitted at other times. The identity of the eggs collected was later verified by microscopic examination of the pattern of chorionic sculpturing, using the technique of Craig (1955).

The physiological age of some females collected at oviposition sites was determined by examination of the ovaries (see Detinova, 1962). This allowed us to distinguish between "young" females (i.e., those that had not yet laid eggs) and "old" females (those that had already done so).

OVIPOSITION BEHAVIOR

The following observations refer to *Aedes nigripes,* which oviposits exposed to view. Oviposition by *A. impiger* was not witnessed.

Ovipositing females (Fig. 1) walk slowly over insolated surfaces, trailing the tip of the abdomen over the substrate and stopping every 1–2 cm. at intervals of 2–8 seconds. Many sites are apparently tested and rejected during the halts, but in other

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Fig. 1. Female of *Aedes nigripes* ovipositing at pond 11 (the wings are about 4 mm. long). Many black eggs already lie on the site. Hazen Camp, Ellesmere Island, 6 August 1963. (Photo: R. E. Leech)

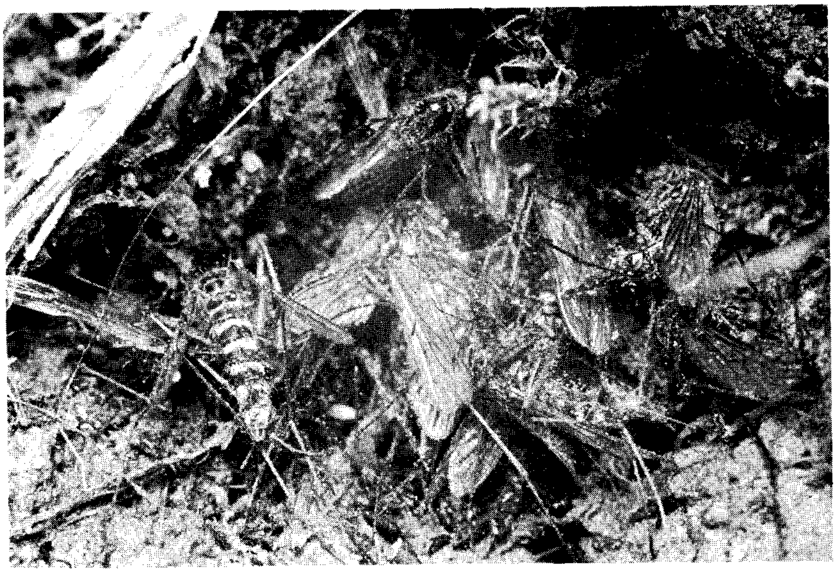

Fig. 2. Dead females of *Aedes nigripes* at an oviposition site late in the summer (a wing is about 4 mm. long). Pond 2, Hazen Camp, Ellesmere Island, 31 July 1963. (Photo: R. E. Leech)

sites a single whitish egg is laid. (This soon turns black.) The behavior of females leads one to suppose that substrate acceptability depends partly on the existence of minor irregularities of surface texture which intercept the probing tip of the abdomen. During oviposition the antennae are held erect, the proboscis projects anteriorly, and the hind-legs are usually held free of the substrate (Fig. 1). Females intermittently rub the abdomen and wings with the hind-legs, or the antennae and proboscis with the fore-legs.

Despite the persistent ambulatory movement of females, eggs are clustered; this is due to several factors (considered in the next section) that cause a limited number of sites to be preferred for oviposition. Thus females can often be seen in large numbers jostling each other on what thus appear to be particularly favored surfaces. Old ovipositing females are normally sluggish and not easily disturbed; young ovipositing females take to flight promptly if disturbed although they seldom fly far. Some fall prey to spiders, which are frequently active on insolated oviposition sites: on one occasion a lycosid spider female, *Tarantula exasperans* Cambridge, was found carrying a freshly captured gravid female of *A. nigripes.* The mosquito (which had a punctured thorax) was slung, ventral surface uppermost, beneath the spider's body.

Later in the season, e.g., August in 1963, dead females were found on the oviposition sites (Fig. 2); many of these females had completed the laying of their current batch of eggs.

PROPERTIES OF OVIPOSITION SITES

Numerous observations of living and dead females on oviposition sites and collections of eggs from different microhabitats allow us to characterize suitable oviposition sites.

GENERAL. *Aedes impiger* lays its eggs, up to several meters away from the current water level, in narrow crevices in the soil, usually those more or less lined with moss, and 5–20 mm. below the ground surface. Eggs are usually clustered and laid in the moss at the level of the moss-soil interface; but inside very narrow cracks, they may be applied to dead leaves, etc. Suitable soil crevices are usually localized and occur most frequently in hummocky areas where the soil texture is fine enough for cracking to occur as the surface begins to dry out. Around several ponds at Hazen Camp no oviposition sites suitable for *A. impiger* were found.

Aedes nigripes lays its eggs, usually 5–10 cm. above the prevailing water level and sometimes up to 2 m. away, on moss or soil surfaces, on silt-covered moss or on bases of stems of plants such as *Carex.* Gravelly sites are apparently not used. Minor irregularities of the texture of the surface apparently encourage oviposition.

MOISTURE. *Aedes nigripes* will oviposit only close to free water, although this need not be extensive. The sites chosen are sometimes waterlogged just below the surface but are never dry or loosely composed. *Aedes impiger,* on the other hand, appears to oviposit in association with moist soil rather than water. The characteristic position of eggs at the moist soil-moss interface supports this interpretation. *A. impiger* may place its eggs some distance above the water; it avoids drier sites but requires the texture of the substrate to be firm and not waterlogged.

WIND. Eggs of both species are laid mainly in areas sheltered from wind. Bank contour occasionally provides such shelter, but beds of emergent *Carex* in shallow water adjacent to the banks normally provide protection for sites favored by ovipositing females (Fig. 3). The *Carex* beds give shelter from wind if they lie 1 m. or less away from shore, but if they remain dense closer to shore than about 30 cm. the pond margin may be obscured or shaded, which appears to render it less suitable for oviposition. The correlation of oviposition with such shelter was confirmed by egg distributions at more than 30 ponds; this correlation results in a

Fig. 3. *Aedes nigripes:* typical oviposition sites sheltered, but not shaded, by emergent *Carex* near the shore (the white rule is 15 cm. long). (a) Pond 76; (b) Pond 13. Hazen Camp, Ellesmere Island, 12 August 1963. (Photo: P. S. Corbet)

marked restriction of the areas in which eggs are found. It may be noted that these beds of *Carex,* and the dead stems that often lie in the water to shoreward of them, diminish disturbance by wind of the water surface near shore and so lessen or eliminate ripples impinging on or below the oviposition sites.

TEMPERATURE. Females oviposit on the warmest sites available. They have only been seen to lay eggs in direct sunshine; moreover that angle of slope is favored which is most closely normal to the sun's rays, and so becomes warmest, at the time of laying. No eggs were found on very gently sloping pond margins. The contour of a pond margin therefore affects shading and slope, and the height and density of *Carex* near or on the bank also determines whether oviposition will be prevented by shading. In addition, eggs arc laid only on slopes which face the sun at the warmest times of the day as indicated in the following section. These direct and indirect temperature effects greatly limit the number of sites that receive eggs; accordingly the density of eggs can sometimes be very high (Fig. 4). The temperature at the ground surface of sites of suitable slope and solar aspect may reach 92° F (33.3° C), and usually exceeds 70° F (21.1° C) during the middle of a sunny day (Corbet 1967, table II, figs. 12, 13 and 15). Corresponding screen-air temperatures very rarely reach 60° F (15.6° C) (Corbet 1967, table II).

DIEL PERIODICITY OF OVIPOSITION

Since females lay eggs only when directly insolated, oviposition at a given time of day is confined to surfaces which more or less face the sun at that time. Collections of eggs made around pond margins in 1963 showed that eggs were distributed unevenly with respect to solar aspect and hence to the hours at which they were laid: oviposition of *A. nigripes* is greatest at solar noon, and that of *A. impiger* in the mid afternoon (Corbet 1966b). These temporal patterns of oviposition correspond with the patterns of global radiation at the ground surface, and of temperature in the superficial soil layers respectively, which in turn correspond with the oviposition sites of the two species. It is therefore very likely that females respond exogenously to prevailing ambient temperature during oviposition. Qualitative observations of females laying eggs on pond margins, and on the sides of partly inundated mounds, also show that greatest oviposition activity of *A. nigripes* occurs near solar noon. This is consistent with the fact that disproportionately few gravid females feature in trap catches of flying adults during cool, overcast weather (Corbet and Danks 1973).

DISCUSSION

The distribution of mosquito eggs around the margins of ponds in this high-arctic area is strikingly discontinuous. *Aedes impiger* oviposits in crevices, a not infrequent trait in mosquitoes (see Mattingly 1969), and *A. nigripes* oviposits on the ground surface near free water, partly in response to irregularities in the substrate (cf. Wallis 1954, and Barr and Azawi 1958, for other *Aedes* spp.). Oviposition in both species is reduced or curtailed during low temperatures and wind.

Eggs are laid only in certain moist sites that are sheltered from wind but not shaded by contour or vegetation; eggs are laid only on slopes that face the sun during the warmest time of the day; and they are laid preferentially on slopes that are more or less normal to the sun's rays. Eggs are accordingly confined to a relatively small number of fortuitously favorable sites on the northern margins of ponds or on the southern sides of mounds or shoreline irregularities in or near ponds. We may suppose that the number of eggs laid near a given pond may depend also on the availability nearby of resting sites, such as stands of *Carex,* suitable for gravid females (cf. Service 1971).

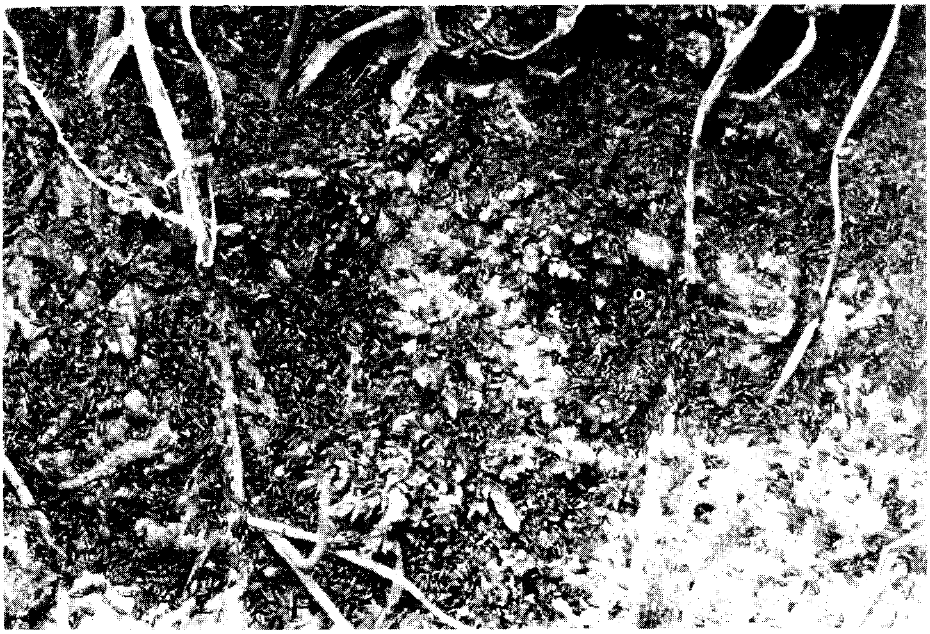

Fig. 4. Eggs of *Aedes nigripes* on a favored oviposition site (an egg is about 1 mm. long). Pond 11, Hazen Camp, Ellesmere Island, 6 August 1963. (Photo: R. E. Leech)

The behavior of ovipositing females results in a highly clumped distribution of eggs, some ponds apparently receiving no eggs even though they may otherwise be suitable as habitats for larvae and pupae. The position of eggs ensures that most of them, especially those of *A. nigripes,* will be inundated early during the thaw. Their restriction to the warmest sites in summer means that they are located in the spots that first become free of snow in spring, and thus that the eggs hatch at the earliest time possible in each pond (Corbet 1964). A further consequence is that the hatch of eggs in a given area is more closely synchronized than if they were less aggregated.

Since mosquito activity at high latitudes is greater at higher temperatures within the normal diel range, the preferences of females for the warmest sites presumably leads to oviposition being completed as rapidly as possible under given weather conditions. Some or all of the eggs are sometimes retained, especially in *A. impiger* (Corbet and Danks 1973), eventually producing relict eggs, which in a temperate mosquito that has been studied seem to occur more frequently at low temperatures (Hitchcock 1968). Selection by arctic species of the warmest site in a habitat may therefore help to reduce the incidence of egg retention. More rapid oviposition in warm sites would also shorten the interval between successive gonotrophic cycles especially when associated with basking by females not yet gravid (see Corbet 1965).

Some of the stimuli that by inference are used in the selection of oviposition sites by these northern mosquitoes, e.g., the moisture content of the substrate (Knight and Baker 1962), are the same as for more southern species (Clements 1963). There are however certain differences, the most striking of which is that temperature seems to play the dominant role in determining the distribution of eggs in the arctic.

The responses of these high-arctic mosquitoes are finely tuned to microclimate.

The importance of temperature for egg-laying activity and for larval development subsequent to egg hatch suggests that, like so many attributes of insects at high latitudes (Downes 1965), the oviposition behavior described here reflects adaptations to the low summer temperature and to its high variability.

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