

SELECTIVITY BY SIX SNOW-MELT MOSQUITO SPECIES FOR LARVAL HABITATS IN QUEBEC SUBARCTIC STRING BOGS

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ABSTRACT. Spatial distribution of the larval populations of 6 snow-melt mosquito species for several vast string bogs of the High-subarctic area of Lake Delorme, Québec (55°00'N; 69°58'W) was analyzed using a reciprocal averaging (RA) analysis and a cluster analysis. Results of these analyses indicate that the vegetation of the bog ridges may be a useful indicator of the environmental features. *Aedes excrucians* and *Ae. riparius* are highly correlated with the *Carex rostrata* vegetal unit; *Ae. hexodontus* and *Ae. decticus* with the *Carex limosa*

unit; *Ae. canadensis* with the *Chamaedaphne calyculata* unit and *Ae. punctor* with the *Picea mariana* and *Carex oligosperma* units. The RA analysis also indicates that the mosquito larval community of shallow water-filled hollows is more related to the ridge vegetation unit giving a general physiognomy to the habitat rather than the size or vegetation of the shallow pool itself. Results are discussed taking in account the high potential selectivity shown by the females for their oviposition sites.

Our previous research showed that mosquito species, qualitatively and quantitatively, exhibit definite selectivity in the choice of their larval habitats (Maire and Aubin 1976, Maire et al. 1979). Surveys from 1974 across the Quebec-Labrador peninsula (Maire 1980, Maire and Aubin 1980) confirmed that the vegetation analysis of the wetlands is a very useful method to define, characterize and map larval habitats of mosquitoes. This was previously suggested by Rioux et al. (1968), Pautou et al. (1973) and, but with less evidence, by Jenkins and Knight (1950, 1952). Finally, we emphasized that there is a typical mosquito community for a particular vegetal unit (Maire 1977, Mailhot and Maire, 1978, Maire and Aubin 1976, 1980; Maire et al. 1979, Tessier et al. 1981).

During 1977, we made a survey in the Lake Delorme area, west of Schefferville, Québec (55°00'N; 69°55'W). Peatlands in this high-subarctic area are very abundant. From a general point of view subarctic peatlands are composed of bogs and fens of the string type. These patterned bogs have more or less parallel bog ridges separated by shallow water-filled depressions; the ridges built up of *Sphagnum* and often supporting a dense vege-

tation with ericaceous shrubs and stunted trees. These vast bogs may be several kilometers long, with a longitudinal declivity of about 3 m per 1000 m (Goyette and Maire 1980).

As a result of this structure, string bogs are composed of a succession of topographical levels from a center up to the periphery. Anyone observing such string bogs may easily note that the vegetation of the ridges also presents a succession of vegetal communities, generally with one or 2 dominant plants providing a general physiognomy to each level of this vast staircase. This vegetation is easy to map from aerial photographs (Tessier et al. 1981). Within each of these ridge vegetal units is a secondary pattern of more or less aligned shallow pools having their own aquatic vegetal and mosquito communities. The first difficulty when sampling mosquito larvae in a string bog is to determine the most typical vegetation profile in order to make an objective characterization of the mosquito habitats. Indeed, in the case of string bogs, it is more questionable to consider the vegetal units of the ridge only, because of the complexity of the arrangement of the pools included among the ridges.

In a schematic perspective, vegetation

of the shallow pools distributed in a particular topographic level characterized by a typical ridge vegetation corresponds to the ridge vegetation of the previous topographical level (Fig. 1-A). For instance, hollows distributed among *Carex oligosperma* ridge units are characterized by a *Carex limosa* community and hollows distributed among the next higher peripheral ridges characterized by *Chamaedaphne calyculata* will be covered by a *Carex oligosperma* unit. Field observations are obviously not so clear. Although larger pools are generally located in the center of bogs, they may also be found at higher peripheral levels among shallower pools

(Fig. 1-B). For these reasons string bogs are interesting study areas to test the degree of selectivity of the snow-melt mosquito species in the choice of their ovipositing and larval sites.

Goyette and Maire (1980) previously investigated differences in species composition, relative abundance and density of larval mosquito populations found in inundated caribou tracks crossing 2 bog habitats with small shallow pools. Statistically they found no appreciable differences in these characters between these sites. On the other hand, Maire et al. (1979) observed species discrimination between the salt-, brackish- or fresh-water

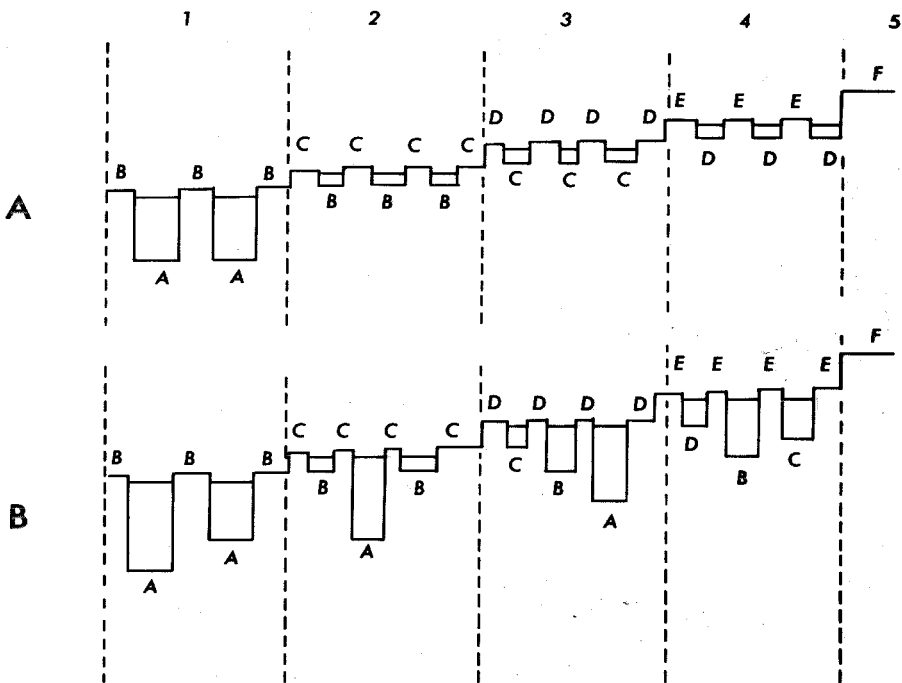


Fig. 1. Theoretical (1-A) and observed (1-B) topographical transects across a subarctic string bog. Above each profile: vegetation of the ridges; below: vegetation of the water-filled hollows. Each letter corresponds to a vegetal unit. Roman figures: topographic levels.

habitats along a tidal topographical gradient. No discrimination was found between the different sizes of the numerous shallow ice-made pans distributed among each of these habitats of the tidal marshes of southeastern James Bay.

In this paper, we attempt to analyze the spatial distribution of the mosquito species in string bogs. Furthermore, we attempt to discern what is the best ecological indicator of the larval habitats—vegetal communities of the ridges or vegetal communities of the pools distributed among these ridges; vegetation being the most convenient biological indicator for use in areas where logistics are difficult. In other words, are mosquito species of these bogs considering each shallow pool as a well defined habitat or considering rather the set of pools distributed within a particular topographic level as a homogeneous habitat (as defined by its ridge vegetal unit)?

MATERIALS AND METHODS

Mosquito larvae were sampled with a 1 liter dipper from the first week of June (first-instar larvae) to the first week of July 1977 (fourth-instar larvae and pupae). For each mosquito sample, the specimens were counted and third- and fourth-instar larvae were identified from Wood et al. (1979). Other larvae were reared until identifiable (Goyette and Maire 1980). Specimens of each species were verified by D. M. Wood (Biosystematics Research Institute, Ottawa) and voucher specimens lodged both at our laboratory and at the Canadian National Collection (CNC), Ottawa. For this study, only samples with all specimens identified were considered. During June and July, a vegetation analysis was made using classic phytosociological methods (Guinochet 1973).

Mosquito larvae in their natural habitats do not have a random distribution and present a clumped or aggregated pattern (contagious distribution) (Tessier et al. 1981). As suggested by Elliott (1979)

and Green (1979), it is important to transform such rough data for standard statistical analysis. For contagious distributions, the best and most commonly used transformation consists of replacing x by $\log(x + 1)$ (when there are 0 counts).

Thirty-eight mosquito samples were submitted to a reciprocal averaging (RA) analysis which is a multivariate method (Benzecri 1973, Hill 1973). Its general use is to reveal correspondence between 2 kinds of information such as species and samples (Gauch et al. 1977). It is a contingency table analysis comparing the different descriptions of a first set of descriptors (the lines of the table, *i.e.* the mosquito samples) with descriptions of a second set of descriptors (the columns of the table, *i.e.* the mosquito species). Thus, this is a method preserving in the factorial space the chi-square distance between the lines and columns of a contingency table (Legendre and Legendre 1979).

In other words, the n lines of the matrix may be considered as n points of a space with p dimensions and the p columns as p points of a space with n dimensions. The reference system illustrating this distribution is composed of the first 2 or 3 axes of an ellipsoid indicating a multi-dimensional normal distribution. Thus, the first axis or *factor* may be viewed as the single best summary of linear relationships exhibited in the data, the second factor as the second best linear combination of variables, under the condition that the second axis is orthogonal to the first. The percentage attributed to the first axis indicates the part of the total inertia (or variance) explained by this axis.

Hypotheses formulated correspond to the 2 questions:

- 1) Are the mosquito species discriminating between the different types of habitats which succeed each other from the center to the periphery of the bogs, as characterized by the ridge vegetation units giving their general physiognomy to each topographic level (for instance *Carex limosa* and *Carex rostrata* units, short- and tall-grass lands respectively)?

2) Are these differences significant in the abundance and specific composition of the mosquito populations of shallow pools having the same ecological characteristics (size, depth, vegetation composition), even if they are distributed in several of the previously defined levels?

Depending on these 2 questions, our successive hypotheses are:

- 1) The mosquitoes discriminate between the ridge vegetal units which succeed each other from the center to the periphery of the bogs;
- 2) The mosquitoes discriminate between the types of shallow pools distributed across a bog depending on their general structure (size, depth, vegetation composition), whatever the ridge vegetal unit in which these pools are located.

The first hypothesis refers to the general distribution of the mosquitoes in the general habitat (discernable at the 1:10 000 cartographic scale). The second hypothesis refers to the distinctness of the habitat selection by the mosquito species from one shallow pool to the other (cartographic scale of 1:100 approximately).

For the RA analysis, only the mosquito samples were used. However, to rapidly interpret results of the analysis, a symbol corresponding to the ridge vegetation unit where each sample was made was assigned to each of 32 mosquito samples (for instance, the 5 mosquito samples made in a *Carex rostrata* unit are labeled CR1 to CR5). To test the second hypothesis, a distinctive symbol (N1 to N5) was assigned to 6 mosquito samples corresponding to 6 shallow pools having the same vegetation composition (*Nuphar variegatum* and *Menyanthes trifoliata*) but located in 3 consecutive levels: the *Carex limosa* unit (3 samples), the *Carex oligosperma* unit (1 sample) and the *Chamaedaphne calyculata* unit (2 samples).

The mosquito sample data were also submitted to a cluster analysis on variables using the BMDP-1M program (clustering by the averaging distance method).

RESULTS AND DISCUSSION

Six snow-melt *Aedes* species were present in the string bogs studied: *Aedes canadensis* (Theobald), *Ae. decticus* Howard, Dyar and Knab, *Ae. excrucians* (Walker), *Ae. hexodontus* Dyar, *Ae. punctor* (Kirby) and *Ae. riparius* Dyar and Knab. The previously distinguished ridge vegetal units were:

- 1) The *Carex rostrata* unit (5 samples) situated in the center of the vast fens, where water is flowing at times, especially during springtime. Pools are wide (about 14,000 m²) but not deep (from 0.02 m to 0.30 m), with a water coverage of about 75% of the total area covered by this vegetal unit;
- 2) The *Carex limosa* unit (7 samples), with also numerous wide but shallow pools (about 1500 m²) with a water coverage of about 65% of the total surface;
- 3) The *Carex oligosperma* unit (9 samples), the *Chamaedaphne calyculata* unit (5 samples) and the *Betula glandulosa* unit (3 samples), a mixed vegetal association of the fens. These 3 vegetal groups have about the same pattern of shallow pools, with a pool surface of about 20 m² and a percentage of water coverage of about 33%;
- 4) The *Picea mariana* and *Chamaedaphne calyculata* unit (3 samples), an open-forested vegetal unit, with only 8% of water coverage made up by very small-sized pools (<1 m²).

Results of the RA analysis are presented in Fig. 2, where the observations (the mosquito samples) and the variables (the 6 mosquito species) are plotted according to the first 3 axes (or factors) with 43.31%, 29.39% and 19.30% of the total inertia respectively.

These results raise several comments. First, the RA analysis corroborates that the vegetation may be a useful integrator of the environmental features in a site. In Fig. 2, the mosquito samples (Q-type factor analysis) are grouped (same symbol shape) according to the initial ridge vegetal units where they were collected. It is particularly evident for the *Carex rostrata*

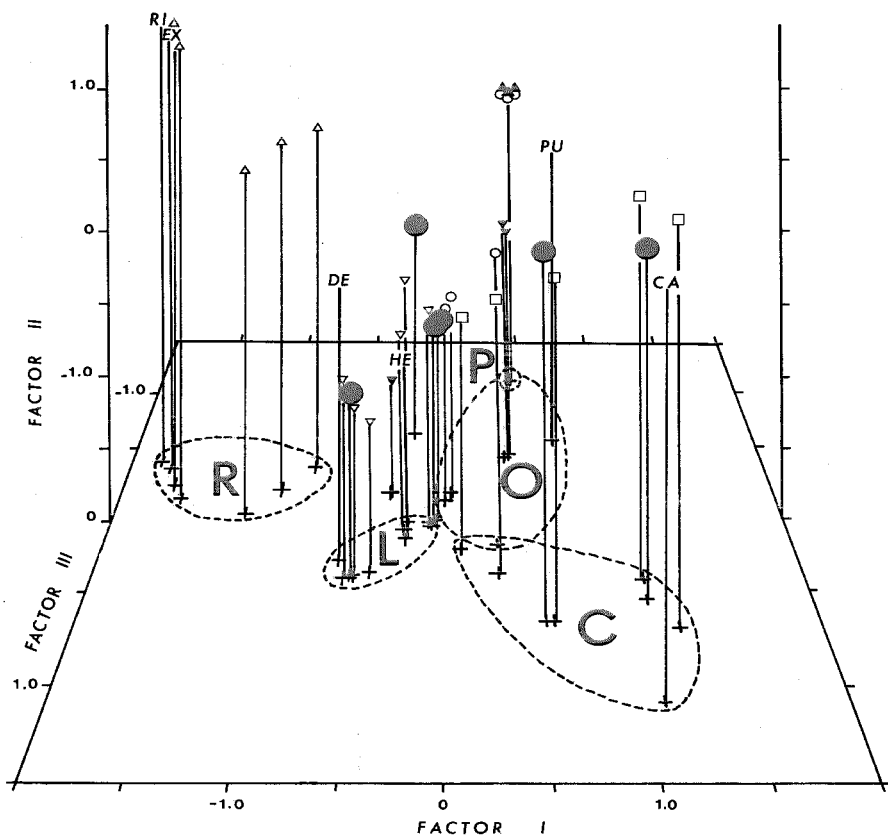


Fig. 2. Mosquito larval samples (symbols) distributed in a three-dimensional ordination space for 6 mosquito species (letters). Observations and variables are plotted in the space defined by the first 3 factors of the RA analysis.

Legend: large closed circles correspond to 6 mosquito samples collected in 6 shallow pools characterized by the same distinctive vegetation; symbols attributed to the other samples correspond to the ridge vegetal unit in which they were collected (open triangle: *Carex rostrata*; closed triangle: *Picea mariana*; open reversed triangle: *Carex limosa*; closed reversed triangle: *Betula glandulosa*; open square: *Chamaedaphne calyculata*; open circle: *Carex oligosperma*).

R = *Carex rostrata* group; L = *Carex limosa* group; O = *Carex oligosperma* group; C = *Chamaedaphne calyculata* group; P = *Picea mariana* group; CA = *Ae. canadensis*; DE = *Ae. decticus*; EX = *Ae. excrucians*; HE = *Ae. hexodontus*; PU = *Ae. punctor*; RI = *Ae. riparius*.

(R), *Carex limosa* (L), *Chamaedaphne calyculata* (C) and *Picea mariana* (P) units, less evident for the *Carex oligosperma* (O) unit (not at all for the *Betula glandulosa* unit). As observations in this analysis are defined from the specific abundances of each mosquito species, we may conclude that there is a good correspondence between the vegetal units and their respective mosquito larval populations.

RA analysis also indicates (R-type factor analysis) that there is a strong bond between the mosquito species themselves and the vegetal units. Thus, *Ae. riparius* (RI) and *Ae. excrucians* (EX) are sharply correlated with the *Carex rostrata* unit; *Ae. hexodontus* (HE) and *Ae. decticus* (DE) with the *Carex limosa* unit; *Ae. punctor* (PU) with the *Picea mariana* and *Carex oligosperma* units and *Ae. canadensis* (CA) with the *Chamaedaphne calyculata* unit. Thus the first hypothesis is accepted.

To determine more precisely the degree of correlation among the 6 species, we have also submitted our mosquito sample data to a cluster analysis on the variables (Fig. 3). The dendrogram re-

sulting of the cluster analysis corroborates the strong correlation ($r = .52$) between *Ae. excrucians* and *Ae. riparius*. Moreover it indicates a good correlation ($r = .40$) between *Ae. hexodontus* and *Ae. decticus*. As for *Ae. punctor* and *Ae. canadensis*, there is only a weak correlation, if any ($r = -.18$). *Aedes hexodontus* and *Ae. decticus*, relatively ubiquitous in the open areas of the bogs, present also a secondary good correlation with *Ae. riparius* and *Ae. excrucians*, more riparian species exclusively confined to the *Carex rostrata* unit.

The 6 pools (black circles in Fig. 2) initially distinguished by their distinctive aquatic vegetation only (*Nuphar variegatum* and *Menyanthes trifoliata*), do not form a distinctive habitat for mosquito larvae. They are in fact integrated among the ridge vegetal units where they were naturally distributed. Thus, the second hypothesis cannot be accepted.

In other words, the mosquito larval community of a pool is more related to the ridge vegetation unit giving the general structure to the habitat than to the size or vegetation of the pool itself. That corroborates our previous conclusions about species distributions of the tidal zones of the southeastern James Bay (Maire et al. 1979) and caribou trails (Goyette and Maire 1980).

This last conclusion is of interest because of the high potential selectivity shown by the females for their oviposition sites. Indeed, because it is impossible for the larvae to go from one isolated pool to another, we assume that only the females may choose the sites where larvae will develop. Many entomologists agree on this selectivity. It is important to know how precise the selectivity is, and for subsequent field experiments, to take in account not only the types of pools but moreover the set of pools comprised inside a small habitat, defined and circumscribed by its vegetal composition.

Several authors have been interested in attractant or stimulant factors inducing oviposition site selection by gravid females. The phenomenon no doubt is very complex and, from a general point of

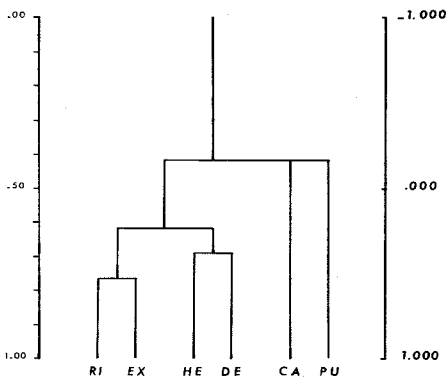


Fig. 3. Dendrogram of the average linkage clustering of the 6 snow-melt *Aedes* analyzed (species abbreviations as in Fig. 2). Left: correlation matrix (scale 0.00 to 1.00) clustering by maximum distance method; right: corresponding correlation scale.

view, one may agree with the remark of McDaniel et al. (1976): "The oviposition response depends on a balance of factors which may interact with a resulting strong influence on site selectivity" (p. 555). On a simplified basis, these factors are of 2 types: those including ecological (or extrinsic) factors, and those including intrinsic factors for the populations.

Ecological factors which have been found to have an attractant effect include light intensity, granulometry and soil moisture conditions, color of the site, presence of decayed organic matter and salinity (Bentley et al. 1976, Olson and Meek 1977, Russo 1978).

On the other hand, several authors attempt, more or less directly, to demonstrate that eggs, larvae or pupae of different mosquito species and genera may produce substances (intrinsic factors) which influence oviposition by gravid females of the same species or of closely related species (Bentley et al. 1976, McDaniel et al. 1979, Kalpage and Brust 1973, Soman and Reuben 1970, Trimble and Wellington 1980, Ikeshoji et al. 1975). These experiments were mainly conducted in the laboratory. In most cases nothing is clearly evident and many questions are left unanswered: are these attractants produced by the larvae or by bacteria or bacterial metabolites; are they quite specific or generally specific; are they volatile or not volatile? Nevertheless, immature stages seem to play a prominent part in the oviposition behavior of the mosquito females.

From an ecological point of view one may assume that vegetation, for female mosquitoes, involves integration of the extrinsic factors necessary for oviposition. In the case of string bogs, several ecological features may explain the habitat differentiation shown for instance by *Ae. punctator* for the forested sites (low incident insolation of the dark-colored ground) or by *Ae. excrucians* for the *Carex rostrata* unit (a minerotrophic habitat where water is slowly circulating). This study shows that mosquito species can discriminate between 3 closely related meadows (the

Carex rostrata, *Carex limosa* and *Carex oligosperma* units). Presently ecologists do not know what ecological factors may explain precisely such discrimination.

It is interesting to note that a new man-made pool is colonized by many mosquito species which usually do not develop together in other natural sites (Jenkins and Knight 1952, Maire and Aubin 1976).

One may consider the larval production of pheromones as an indication for subsequent ovipositing females of the same species that the site has the required successful ecological factors for its offspring. These substances may act as a multiway but strong ecological integrator. This could explain the relatively high selectivity of the species for their larval habitats. These considerations may be helpful as a guide to further experiments which will include both field and laboratory observations, and holistic and reductionist approaches.

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