HABITAT REQUIREMENTS OF MOSQUITO LARVAE

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We studied basic habitat requirements of the mosquito species occurring in Hungary. 1239 samples were taken (mainly around Lake Balaton and in the Tisza Region). Our results showed that the basic indicator variables in the colonization of different mosquito species are: (i) water surface area, (ii) presence of pondweed vegetation, (iii) depth, transparency and temperature of the breeding water. These variables related closely to the regime (permanent or temporary) of the water body. It was confirmed by quantitative ecological analyses that the most important human-biting mosquito species (*e.g. Aedes vexans, Ochlerotatus sticticus, Ochlerotatus annulipes, Ochlerotatus cantans, Aedes rossicus*) usually occur in shallow, quick-warm, regularly drying, clear water bodies with minimal cover of the water surface and without presence of hydrophyta plant species (both in shaded and lightened places).

Key words: mosquitoes, assemblages, aquatic habitat use, pH, temperature, hydrological regime, Hungary.

INTRODUCTION

Presence-absence and size of the populations (spatial and temporal) are determined mainly by the habitat-requirements of the species (Morris, 2003). Several habitat variables (*e.g.* annual temperature, mean temperature of the coldest month, pH, length of the flooded period, size, temperature and vegetation of the breeding site) partake in organization of the larval mosquito assemblages (Becker, 1989; Paradise, 2000; Schäfer, 2004; Fischer & Schweigmann, 2004; Bauer *et al*., 2011). Besides the above mentioned factors some special requirements of mosquitoes are also known. For example, females during egg laying prefer black colour and ignore green colour of artificial containers (Williams, 1962; McDaniel *et al*., 1976; Jones & Schreiber, 1994). Mosquito species show extreme differences in habitat-dependency (Schäfer, 2004; Tóth, 2004; Sattler *et al*., 2005; Alfonzo *et al*., 2005; Azari-Hamidian, 2007).

The above mentioned aspects of the organization of mosquito assemblages have not been studied in detail in Central-Europe, in spite of the fact that this is an important region from a mosquito-control point of view. In this paper we present the aquatic habitat requirements of mosquitoes in Hungary. Many potential factors which may determine the organization of the larval mosquito assemblages in this region have not been researched with quantitative studies before.

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The goal of the study was to determine the aquatic habitat variables important for the colonization of different mosquito species (potential factors are shading, pH, vegetation, length of the water supply).

MATERIAL AND METHODS

Location

We collected 1239 samples in regions (Balaton Region, Lake Tisza) of Hungary being rich in mosquito breeding sites. 591 samples were collected in the Region of Lake Tisza, altitudes of these sites were between 80 and 95 metres height above sea level. Overall extension of the sampled breeding sites around Lake Tisza was 1135 hectares. 648 samples were collected in the Region of Lake Balaton, altitudes of these sites were between 91 and 140 metres height above sea level. Overall extension of the sampled breeding sites around Lake Balaton was 1033 hectares.

Repartition of the samples among the breeding site-types was the following: (1) marshy (reed-bed and sedgy) closed vegetation (MV): 419 samples; (2) marshy (reed-bed and sedgy) closed vegetation with pondweeds (MV+): 266 s.; (3) herb vegetation (HV): 261 s.; (4) lakes (OW): 121 s.; (5) forest vegetation (FV): 146 s.; (6) artificial containers: 26 s.

Sampling methods and timing

In each sampling site 10 square metres quadrat was studied. Sampling of the mosquitoes was carried out with a 20cm-sized-circle straining net. Larvae collected by 2–3 dips were defined as one sample. It means examination of 1 litre breeding water in every site.

Samples were taken between 04 September 2003 and 06 June 2007. The time of the samplings within months was shaped to the temporal importance of the breeding sites [14 samples were taken in February; March (101); April (290); May (171); June (39); July (87); August (225); September (233); October (76); November (3)].

Part of the sampling sites was sampled repeatedly, but many of them were sampled just once only. Merging of the samples taken in the same place in different time is unreasonable, because the ecological factors of the breeding sites (they are usually temporary habitats) can be assigned to the time of the given sampling.

In laboratory 31227 larvae of 30 species were determined. The detected mosquito species and their most important life-characters are listed in Table 1. (nomenclature: Becker *et al*., 2003). After the first mentions the abbreviations of the species names (see Table 1) are used in the text.

Sampled habitat variables

In each sampling site the following habitat variables were recorded: altitude; plant association(s) in the habitat; the most typical plant species of the water and waterside; presence of pondweed vegetation (0/1); cover of the water surface (1–5: 1 = 0%, 2 = 1–20%, 3 = 20–40%, 4 = 40–60%, 5 = 80–100%); pH; temperature, depth, regime (permanent or temporary, 0/1), transparency (in scale 1–5), shading (1–5: 1 = no shaded; 2 = shaded by short grass (< 20 cm), 3 = shaded by tall grass (> 20 cm) or recessing (canals), 4 = opened forest, forest ecotone, 5 = closed forest) of the breeding sites.

Data analysis

Relations between occurrences of mosquito larvae and potential influential habitat variables were studied by Pearson-correlation, logistic regression, multiple regression and canonical correspondence analysis. Binary matrices were analysed by logistic regression, others were analysed by all the methods mentioned. Significant correlations of Pearson-analyses were supervised by Bonferroni technique (acceptance at $p < 0.001$). Database of the recorded plant species was reduced. 348 plant taxa were recorded, out of which 125 were listed in more than 10 samples. Logistic regression (simplex method) was accomplished with these species (presence-absence matrices of the plant and mosquito species were used).

Independent variables of the multiple regression were the density values of all the collected species, dependent variables were the following: altitude, water depth, water transparency, regime (permanent or temporary), presence of the pondweed vegetation, cover of the water surface, shading, temperature and pH of the water. Multicollinearity has to be taken into consideration because of several coherent variables of the regression.

Environmental variables of canonical correspondence analysis were the temperature, pH, transparency, regime (permanent or temporary), shading and depth of the water, cover of the water surface, presence of the pondweed vegetation and altitude.

For the statistical analyses STATISTICA 6.0 (Statsoft, 1995) and PAST (Hammer *et al*., 2001) statistical program packages were used.

RESULTS

Based on the confirmed (Bonferroni technique) results of the Pearson correlation analyses (Table 3) presence of *Ochlerotatus annulipes* (Meigen, 1830), *Anopheles claviger* (Meigen, 1804), and *Culiseta annulata* (Schrank, 1776) is related to breeding sites occurring in submountain regions. On the contrary, presence of *Aedes rossicus* Dolbeshkin, Goritzkaja & Mitrofanova, 1930, *Ochlerotatus flavescens* (Müller, 1764), *Anopheles maculipennis* Meigen, 1818, *Anopheles messeae* Falleroni, 1926, *Anopheles hyrcanus* (Pallas, 1771), *Culex modestus* Ficalbi, 1890, *Uranotaenia unguiculata* Edwards, 1913 is related to low altitude. Multiple regression confirmed the above mentioned relations without

Ochann, Anomes, Anohyr species and showed that *Ochlerotatus dorsalis* (Meigen, 1830) and *Culex martinii* Medschid, 1930 are related to plains (Table 6).

Pearson correlation analyses showed (confirmed by Bonferroni technique) (Table 3) that water transparency influences the density of *Ochann* and *Anocla* – densities of the mentioned species are in ordinal relation with the water transparency. Multiple regression did not confirm these relations, and showed that *Coquillettidia richiardii* (Ficalbi, 1889) is related to cloudy water and *Ochlerotatus sticticus* (Meigen, 1838) is related to clear water (Table 6).

Based on Pearson correlations (confirmed by Bonferroni technique) (Table 3) permanent regime of the breeding water influences positively the density of *Coqric, Anomac, Anocla, Anomes* and *Culmod*. On the contrary, *Aedes cinereus* Meigen, 1818*, Aedvex, Ochann* and *Ochfla* are related to temporary waters. Multiple regression did not confirme this relation in connection with *Anomes* and *Ochfla*. Furthermore, it pointed out that *Culex hortensis* Ficalbi, 1890, *Anomes, Anohyr* connect to temporary waters (Table 6).

Pearson correlation analyses showed (confirmed by Bonferroni technique) (Table 4) that the presence of the pondweed vegetation affects positively the density of *Coqric, Anomac, Culmod*, and negatively the density of *Aedvex* and *Ochfla*. Multiple regression confirmed these relations*,* furthermore it showed that the presence of the pondweed vegetation and the presence of *Ochlerotatus rusticus* (Rossi, 1790), *Aedros* and *Culhor* are in inverse relation, further presence of the pondweed vegetation and the presence of *Culex territans* Walker, 1856 is in ordinal relation.

Correlation analyses (confirmed by Bonferroni technique) demonstrated (Table 4) that the cover of the water surface (mainly cover of *Lemna* spp., *Spirodela*, *Wolffia*) influences the density of the species in differrent ways. Significant positive relations were revealed between the cover of the water surface and the density of *Coqric, Anomac* and *Culmod*, while between the cover of the water surface and the density of *Aedes vexans* (Meigen, 1830)*, Aedcin, Ochann*, *Ochfla* significant negative relations were revealed. Multiple regression confirmed these results and revealed negative relations between the density of *Anohyr, Culex pipiens* Linnaeus, 1758 and the cover of the water surface (Table 6).

Pearson correlation (confirmed by Bonferroni technique) analyses showed (Table 4) that *Ochlerotatus cantans* (Meigen, 1818)*, Ochrus* and *Culann* related to shaded-, half-shaded habitats. Multiple regression confirmed these relations and revealed further negative (*Aedcin, Anomac, Anopheles atroparvus* Van Thiel, 1927) and positive (*Anohyr, Ochsti*) relations between shading and density of the mosquito species (Table 6).

Pearson correlation analyses (confirmed by Bonferroni technique) (Table 4) of the densities and pH showed that *Ochlerotatus refiki* (Medschid, 1928) and *Ochann* relate to basic, *Culiseta morsitans* (Theobald, 1901) to acidic waters.

Multiple regression showed rather different results. It marked *Aedvex, Aedros, Ochlerotatus cataphylla* (Dyar, 1916), *Ochlerotatus caspius* (Pallas, 1771), *Ochrus, Ochdor, Anomac, Culhor, Uraung* as species related to basic pH, and *Ochsti, Anocla, Culpip, Culter*, *Culann* as species related to acidic pH (Table 6). The study sites are situated in large natural habitats and the well-researched treeholes (e.g. Bradshaw & Holzapfel, 1991; Sota *et al*., 1994; Dahl & Blackmore, 2001) characterized by special water chemistry were not sampled.

Table 1

Abbreviations and significant life-strategy features of the collected mosquito species
[Legends: OS = oviposition site (WS: water surface; DS = dry surface); HS = hibernation state (E: egg; L: larva, F: female); NG = number of generations within year (M = multivoltine, U = univoltine)]

Species	**Abb.**	**OS**	**HS**	**NG**
Aedes vexans (Meigen, 1830)	*Aedvex*	DS	E	M
Aedes cinereus Meigen, 1818	*Aedcin*	DS	E	M
Aedes rossicus Dolbeshkin, Goritzkaja & Mitrofanova, 1930	*Aedros*	DS	E	M
Ochlerotatus excrucians (Walker, 1856)	*Ochexc*	DS	E	U
Ochlerotatus annulipes (Meigen, 1830)	*Ochann*	DS	E	U
Ochlerotatus cantans (Meigen, 1818)	*Ochcan*	DS	E	U
Ochlerotatus caspius (Pallas, 1771)	*Ochcas*	DS	E	M
Ochlerotatus cataphylla (Dyar, 1916)	*Ochcat*	DS	E	U
Ochlerotatus sticticus (Meigen, 1838)	*Ochsti*	DS	E	M
Ochlerotatus rusticus (Rossi, 1790)	*Ochrus*	DS	L	U
Ochlerotatus refiki (Medschid, 1928)	*Ochref*	DS	E	U
Ochlerotatus flavescens (Müller, 1764)	*Ochfla*	DS	E	U
Ochlerotatus nigrinus (Eckstein, 1918)	*Ochnig*	DS	E	U
Ochlerotatus dorsalis (Meigen, 1830)	*Ochdor*	DS	E	U
Coquillettidia richiardii (Ficalbi, 1889)	*Coqric*	WS	L	U
Anopheles maculipennis Meigen, 1818	*Anomac*	WS	F	M
Anopheles claviger (Meigen, 1804)	*Anocla*	WS	L	M
Anopheles messeae Falleroni, 1926	*Anomes*	WS	F	M
Anopheles hyrcanus (Pallas, 1771)	*Anohyr*	WS	F	M
Anopheles algeriensis Theobald, 1903	*Anoalg*	WS	L	M
Anopheles atroparvus Van Thiel, 1927	*Anoatr*	WS	F	M
Culex modestus Ficalbi, 1890	*Culmod*	WS	F	M
Culex pipiens Linnaeus, 1758	*Culpip*	WS	F	M
Culex territans Walker, 1856	*Culter*	WS	F	M
Culex torrentium Martini, 1924	*Cultor*	WS	F	M
Culex hortensis Ficalbi, 1890	*Culhor*	WS	F	M
Culiseta morsitans (Theobald, 1901)	*Culmor*	DS	L	U
Culex martinii Medschid, 1930	*Culmar*	WS	F	M
Culiseta annulata (Schrank, 1776)	*Culann*	WS	F	M
Uranotaenia unguiculata Edwards, 1913	*Uraung*	WS	F	M

Table 2

Number of positive samples and habitat requirements of the recorded mosquito species based on the measured data (minimum, modus and maximum values)

Species	Nr of samples	Water depth (cm)	Water transparency (scale)	Water pH	Water temperature (°C)	Cover of the water surface (scale)	Shading (scale)
Aedes vexans	251	3-(20)-60	1-(3)-5	6.7-(8.5)-10.2	7.8-(14.1)-28.7	1-(1)-4	1-(3)-5
Aedes cinereus	169	3-(20)-60	1-(3)-5	6.7-(8.5)-11.6	6.2-(15.5)-27.9	1-(1)-4	1-(3)-5
Aedes rossicus	20	10-(20)-40	1-(3)-4	7.5-(8.5)-9.0	8.3-(11.6)-17.2	1-(1)-3	2-(3)-4
Ochlerotatus excrucians	32	5-(15)-40	2-(3)-5	6.7-(6.9)-9.4	8.3-(14.2)-20.2	1-(1)-4	2-(3)-4
Ochlerotatus annulipes	224	3-(20)-60	1-(3)-5	6.7-(8.5)-10.9	7.8-(11.3)-26.3	1-(1)-5	1-(3)-5
Ochlerotatus cantans	62	5-(15)-40	1-(3)-5	6.8-(8.4)-10.9	9.1-(14.8)-24.6	1-(1)-5	1-(4)-5
Ochlerotatus caspius	117	3-(10)-45	1-(3)-4	6.7-(8.5)-9.5	8.3-(23.4)-30	1-(1)-4	1-(2)-4
Ochlerotatus cataphylla	34	5-(20)-40	1-(3)-5	6.7-(8.2)-10.9	9.1-(12.4)-21.3	1-(1)-3	2-(3)-4
Ochlerotatus sticticus	122	5-(20)-50	2-(3)-5	6.8-(8.5)-9.3	9.3-(22.3)-28.5	1-(1)-4	1-(3)-5
Ochlerotatus rusticus	51	3-(20)-50	1-(3)-5	6.7-(8.2)-12.1	6-(15.2)-26.3	1-(1)-5	2-(3)-5
Ochlerotatus refiki	5	3-(30)-30	3-(4)-5	8.2-10.2	6.6-(11.8)-22.3	1 (1)	3-(4)-4
Ochlerotatus flavescens	71	5-(15)-45	1-(3)-4	6.7-(8.4)-11.6	7.8-(11.3)-26.3	1-(1)-3	1-(3)-4
Ochlerotatus nigrinus	2	25-30	3-(3)	8.5-(8.5)	12.3-(12.3)	1-(1)	2-(2)
Ochlerotatus dorsalis	13	10-(20)-35	1-(2)-3	7.9-(8.1)-11.6	8.1-23.3	1-(1)-4	1-(2)-3
Coquillettidia richiardii	35	15-(20)-75	2-(3)-5	6.2-(8.2)-9.3	8.2-(13.2)-25.8	1-(4)-5	2-(3)-4
Anopheles maculipennis	464	0.2-(20)-120	1-(3)-5	6.2-(8.3)-12.1	8.2-(21.6)-30.2	1-(1)-5	1-(3)-5
Anopheles claviger	95	7-(20)-120	2-(3)-5	6.8-(8.1)-10.7	7.1-(9.6)-23.7	1-(2)-5	1-(3)-5
Anopheles messeae	52	0.2-(20)-70	2-(3)-5	6.6-(8.9)-10.4	12.3-(20.1)-28.5	1-(1)-5	1-(3)-5
Anopheles hyrcanus	16	5-(20)-60	2-(3)-4	7.2-(9.3)-10.4	8.7-26.5	1-(1)-4	2-(3)-4
Anopheles algeriensis	4	30-(30)-60	3-(3)-4	8.6-(10.4)-10.4	18.8-22.3	1-(3)-3	2-(3)-4
Anopheles atroparvus	8	10-(10)-40	2-(3)-3	8.2-(9.0)-9.0	11.8-26.3	1-(1)-3	1-(2)-2
Culex modestus	189	0.2-(20)-120	1-(3)-5	6.1-(8.2)-14.1	8.7-(21.6)-28.8	1-(1)-5	1-(3)-5
Culex pipiens	492	3-(10)-120	1-(3)-5	6.2-(8.3)-14.1	6.2-(24.1)-33.2	1-(1)-5	1-(3)-5
Culex territans	111	5-(20)-120	2-(3)-5	6.2-(7.4)-14.1	7.1-(20.7)-33.2	1-(1)-5	1-(3)-5
Culex torrentium	1	30	4	8.6	22.3	1	2
Culex hortensis	23	5-(10)-60	2-(3)-4	7.0-(8.5)-10.1	8.2-(25.8)-29.5	1-(1)-5	1-(3)-4
Culiseta morsitans	17	10-(20)-50	1-(3)-5	6.8-(7)-8.2	7.1-17.7	1-(2)-4	2-(3)-4
Culex martinii	1	40	5	8.1	13.8	3	3
Culiseta annulata	213	5-(20)-120	1-(3)-5	6.2-(8.4)-14.1	7.8-(20.1)-26.1	1-(1)-5	1-(3)-5
Uranotaenia unguiculata	61	5-(10)-80	2-(3)-5	6.2-(8)-14.1	13.2-(21.6)-30.4	1-(1)-5	1-(3)-5

Table 3

Correlations between densities of the mosquito species and the recorded habitat variables I. [Significant values of the correlation analyses are bold; significant values were confirmed by Bonferroni technique (acceptance at $p < 0.001$) are bold and marked (*)]

Species	Altitude		Water depth		Water transparency		Regime (t/p)	
Aedvex	0.0358	p=0.2080	-0.0284	p=0.3180	**0.0738**	**p=0.0090**	**-0.0965**	**p=0.0010***
Aedcin	0.0273	p=0.3380	-0.0179	p=0.5300	-0.0229	p=0.4200	**-0.1490**	**p=0.0001***
Aedros	**-0.0800**	**p=0.0050**	0.0059	p=0.8350	-0.0069	p=0.8090	-0.0484	p=0.0880
Ochexc	0.0514	p=0.0700	-0.0169	p=0.5520	0.0046	p=0.8720	**-0.0598**	**p=0.0350**
Ochann	**0.1149**	**p=0.0001***	**-0.0614**	**p=0.0310**	**0.1421**	**p=0.0001***	**-0.1535**	**p=0.0001***

Table 3

(continued)

Ochcan	0.0545	p=0.0550	-0.0422	p=0.1380	**0.0872**	**p=0.0020**	**-0.0659**	**p=0.0200**
Ochcat	**0.0754**	**p=0.0080**	-0.0303	p=0.2870	0.0397	p=0.1630	**-0.0564**	**p=0.0470**
Ochsti	**0.0715**	**p=0.0120**	-0.0397	p=0.1630	**0.0924**	**p=0.0010**	-0.0523	p=0.0660
Ochrus	**0.0775**	**p=0.0060**	**-0.0703**	**p=0.0130**	-0.0035	p=0.9020	**-0.0680**	**p=0.0170**
Ochref	0.0375	p=0.1870	0.0101	p=0.7230	0.0167	p=0.5560	-0.0328	p=0.2490
Ochfla	**-0.0571**	**p=0.0440**	**-0.0619**	**p=0.0290**	0.0375	p=0.1880	**-0.1155**	**p=0.0001***
Ochnig	-0.0441	p=0.1210	0.0144	p=0.6140	-0.0028	p=0.9200	-0.0273	p=0.3380
Ochdor	**-0.0688**	**p=0.0150**	-0.0043	p=0.8810	**-0.0718**	**p=0.0110**	-0.0505	p=0.0760
Coqric	-0.0205	p=0.4720	**0.1143**	**p=0.0001***	0.0258	p=0.3650	**0.1733**	**p=0.0001***
Anomac	**-0.1980**	**p=0.0001***	**0.0694**	**p=0.0150**	-0.0429	p=0.1320	**0.2519**	**p=0.0001***
Anocla	**0.1651**	**p=0.0001***	**0.1301**	**p=0.0001***	**0.1186**	**p=0.0001***	**0.1468**	**p=0.0001***
Anomes	**-0.0770**	**p=0.0070**	-0.0076	p=0.7880	0.0057	p=0.8410	**0.0710**	**p=0.0130**
Anohyr	**-0.1061**	**p=0.0001***	-0.0153	p=0.5910	0.0002	p=0.9930	0.0314	p=0.2700
Anoalg	-0.0217	p=0.4460	0.0419	p=0.1410	0.0276	p=0.3320	0.0446	p=0.1170
Anoatr	-0.0434	p=0.1270	-0.0157	p=0.5820	-0.0091	p=0.7490	-0.0423	p=0.1370
Culmod	**-0.1604**	**p=0.0001***	0.0299	p=0.2930	-0.0433	p=0.1270	**0.1555**	**p=0.0001***
Culpip	-0.0383	p=0.1780	-0.0509	p=0.0730	-0.0449	p=0.1140	-0.0068	p=0.8110
Culter	0.0137	p=0.6290	**0.0571**	**p=0.0450**	0.0248	p=0.3830	**0.0796**	**p=0.0050**
Cultor	0.0223	p=0.4340	0.0156	p=0.5830	0.0395	p=0.1650	-0.0193	p=0.4980
Culhor	-0.0526	p=0.0640	-0.0270	p=0.3420	0.0399	p=0.1600	-0.0477	p=0.0930
Culmor	**0.0850**	**p=0.0030**	0.0180	p=0.5260	-0.0143	p=0.6160	0.0125	p=0.6610
Culmar	0.0497	p=0.0800	0.0374	p=0.1890	**0.0810**	**p=0.0040**	0.0419	p=0.1400
Culann	**0.1377**	**p=0.0001***	-0.0380	p=0.1820	0.0443	p=0.1190	-0.0362	p=0.2030
Uraung	**-0.1131**	**p=0.0001***	-0.0276	p=0.3320	0.0160	p=0.5740	0.0077	p=0.7860

Pearson correlation analyses (confirmed by Bonferroni technique) (Table 4) between the mosquito larval densities and temperature-values showed that *Anomac, Anomes, Culmod, Culpip, Culhor, Uraung* are related to high water temperature, but *Ochann* and *Anocla* are related to low water temperature. Multiple regression also showed rather different results. It confirmed the results in connection with density of *Anomes* and *Uraung,* but showed several further dependence. Based on this *Aedcin, Ochlerotatus excrucians* (Walker, 1856), *Ochcan, Ochcas, Culter, Culmor*, *Culann* occur in warm waters, *Aedvex, Ochref, Ochcat*, *Ochdor, Coqric, Anoatr* in larval habitats characterized by low temperature (Table 6).

Logistic regression of the presence-absence matrix of the mosquitoes and plant species revealed several positive and negative relations between the occurrences (see Table 5). Mosquito species related to permanent waters (*Anopheles algeriensis* Theobald, 1903*, Anocla, Anohyr*, *Anomac, Anomes, Coqric, Culann, Culmod, Culter, Uraung*) occur usually parallel with hydrophytic marshy plant species (*Alopecurus pratensis, Butomus umbellatus, Calystegia sepium,* *Carex acutiformis, Ceratophyllum demersum, Iris pseudacorus, Typha angustifolia Lythrum virgatum*) and aquatic plants (*Hydrocharis morsus-ranae, Lemna minor, L. trisulca, Salvinia natans, Spirodela polyrhiza*). Whereas occurences of mosquito species related to temporary waters (*Aedcin, Aedvex, Ochann, Ochcan, Ochcas, Ochfla, Ochrus, Ochsti*) show negative correlations with hydrophytic plant species, but occur together with typical species of marshy meadows and grasslands (*e.g. Carex acutiformis, Alopecurus pratensis*).

Canonical correspondence analysis showed that (1) temperature of the breeding site, (2) shading, pH and transparency of the water, and (3) regime (permanent or temporary), depth, water surface cover, presence of the pondweed vegetation are three indicator variables groups which assign the species composition and structural features of the mosquito larval assemblages (Fig. 1).

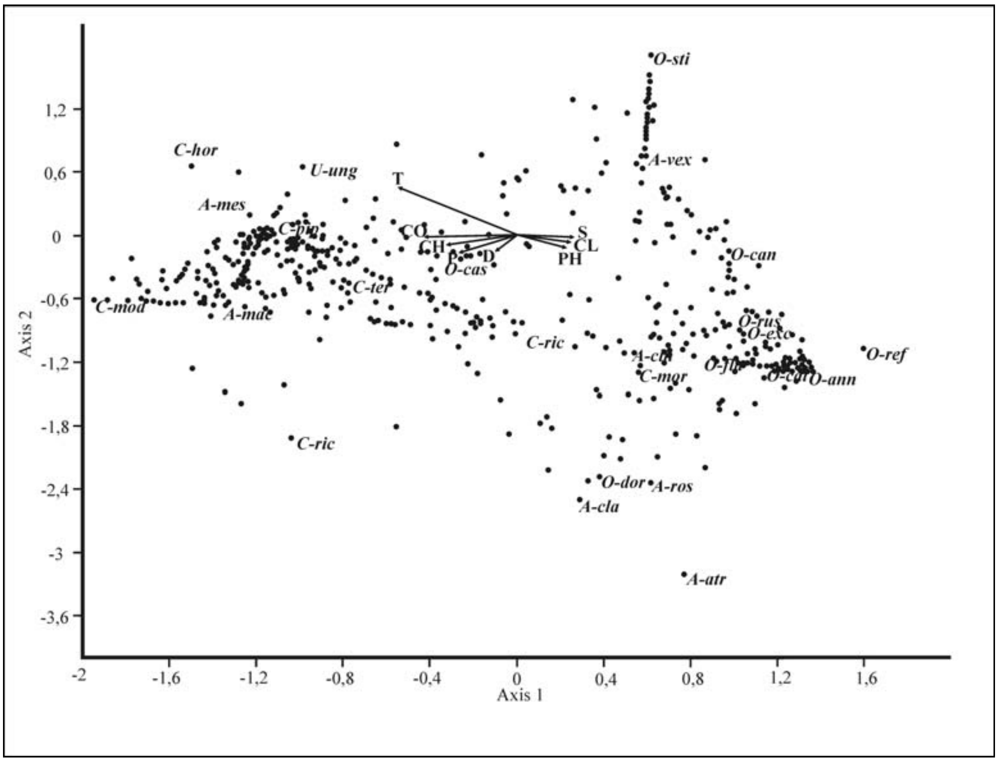

Fig. 1. Based on the results of the canonical correspondence analysis (1) temperature of the breeding site, (2) shading, pH and transparency of the water, and (3) regime, depth, cover of the water surface, presence of the pondweed vegetation are the three indicator variables groups which assign the species composition and structural features of the mosquito larval assemblages.

Table 4

Correlations between densities of the mosquito species and the recorded habitat variables II. [Significant values of the correlation analyses are bold; significant values were confirmed by Bonferroni technique (acceptance at p < 0.001) are bold and marked (*)]

Species	**Pondweed vegetation**		**Cover of the water surface**		**Shading**		**pH**		**Temperature**	
Aedvex	**-0.1072**	**p=0.0001***	**-0.0939**	**p=0.0010***	0.0427	p=0.1330	0.0574	p=0.1140	0.0540	p=0.1370
Aedcin	-0.0513	p=0.0710	**-0.1200**	**p=0.0001***	-0.0306	p=0.2820	**0.0864**	**p=0.0170**	-0.0377	p=0.2990
Aedros	**-0.0740**	**p=0.0090**	**-0.0573**	**p=0.0440**	-0.0209	p=0.4620	**0.0472**	**p=0.1940**	-0.0956	p=0.0080
Ochexc	-0.0341	p=0.2310	-0.0354	p=0.2130	0.0116	p=0.6830	-0.0542	p=0.1360	-0.0575	p=0.1130
Ochann	**-0.0811**	**p=0.0040**	**-0.1495**	**p=0.0001***	**0.0824**	**p=0.0040**	**0.1401**	**p=0.0001***	**-0.1713**	**p=0.0001***
Ochcan	**-0.0781**	**p=0.0060**	**-0.0701**	**p=0.0140**	**0.1049**	**p=0.0001***	**0.0714**	**p=0.0490**	-0.0191	p=0.5990
Ochcat	**-0.0718**	**p=0.0110**	-0.0495	p=0.0810	**0.0733**	**p=0.0100**	0.0165	p=0.6490	**-0.0884**	**p=0.0150**
Ochsti	**-0.0617**	**p=0.0300**	**-0.0562**	**p=0.0480**	**0.0901**	**p=0.0010**	0.0542	p=0.1360	**0.0787**	**p=0.0300**
Ochrus	**-0.0868**	**p=0.0020**	**-0.0596**	**p=0.0360**	**0.1064**	**p=0.0001***	0.0096	p=0.7910	**-0.1084**	**p=0.0030**
Ochref	-0.0409	p=0.1500	-0.0376	p=0.1870	**0.0637**	**p=0.0250**	**0.1181**	**p=0.0010**	-0.0381	p=0.2950
Ochfla	**-0.1040**	**p=0.0001***	**-0.1259**	**p=0.0001***	-0.0348	p=0.2210	**0.1079**	**p=0.0030**	**-0.0862**	**p=0.0170**
Ochnig	-0.0341	p=0.2310	-0.0313	p=0.2710	-0.0456	p=0.1090	0.0220	p=0.5440	-0.0370	p=0.3080
Ochdor	-0.0241	p=0.3970	-0.0417	p=0.1430	**-0.0630**	**p=0.0270**	0.0623	p=0.0860	-0.0582	p=0.1090
Coqric	**0.1267**	**p=0.0001***	**0.1188**	**p=0.0001***	0.0543	p=0.0560	**-0.0995**	**p=0.0060**	-0.0484	p=0.1830
Anomac	**0.1527**	**p=0.0001***	**0.1325**	**p=0.0001***	-0.0556	p=0.0510	0.0430	p=0.2370	**0.2358**	**p=0.0001***
Anocla	0.0131	p=0.6440	**0.0624**	**p=0.0280**	0.0181	p=0.5240	-0.0657	p=0.0700	**-0.1894**	**p=0.0001***
Anomes	0.0446	p=0.1170	0.0475	p=0.0950	0.0042	p=0.8820	**0.0737**	**p=0.0420**	**0.1470**	**p=0.0001***
Anohyr	0.0181	p=0.5260	-0.0156	p=0.5820	0.0355	p=0.2120	0.0641	p=0.0780	0.0565	p=0.1200
Anoalg	0.0635	p=0.0250	0.0126	p=0.6570	-0.0063	p=0.8250	**0.1056**	**p=0.0040**	0.0351	p=0.3340
Anoatr	-0.0245	p=0.3900	-0.0467	p=0.101	**-0.0721**	**p=0.0110**	0.0705	p=0.0520	-0.0484	p=0.1830
Culmod	**0.1301**	**p=0.0001***	**0.1482**	**p=0.0001***	-0.0423	p=0.1370	**0.1206**	**p=0.0010**	**0.1769**	**p=0.0001***
Culpip	-0.0161	p=0.5700	-0.0241	p=0.3960	-0.0095	p=0.7380	-0.0219	p=0.5470	**0.2516**	**p=0.0001***
Culter	0.0514	p=0.0710	**0.0568**	**p=0.0460**	0.0317	p=0.2650	-0.0017	p=0.9620	**0.0903**	**p=0.0130**
Cultor	0.0336	p=0.2380	-0.0221	p=0.4370	-0.0322	p=0.2570	0.0269	p=0.4590	0.0318	p=0.3820
Culhor	-0.0466	p=0.1010	0.0098	p=0.7290	-0.0368	p=0.1960	0.0616	p=0.0900	**0.1468**	**p=0.0001***
Culmor	-0.0325	p=0.2540	0.0298	p=0.2950	0.0106	p=0.7100	**-0.1328**	**p=0.0001***	**-0.0844**	**p=0.0200**
Culmar	-0.0241	p=0.3970	0.0259	p=0.3630	0.0039	p=0.8910	0.0027	p=0.9420	-0.0267	p=0.4620
Culann	-0.0376	p=0.1870	-0.0248	p=0.3840	**0.1142**	**p=0.0001***	-0.0225	p=0.5370	-0.0346	p=0.3410
Uraung	0.0167	p=0.5570	0.0256	p=0.3670	0.0433	p=0.1270	0.0563	p=0.1210	**0.1286**	**p=0.0001***

Table 5

Relations between the presence of the mosquito species and the presence of the plant species based on logistic regression (Simplex method, Chi-square and p values) [Abbreviations of the plant names: Bu_um = *Butomus umbellatus*; Ce_de = *Ceratophyllum demersum*; Hy_mo = *Hydrocharis morsus-ranae*; Le_mi = *Lemna minor*; Le_tr = *Lemna trisulca*; Sa_na=*Salvinia natans*; Sp_po = *Spirodela polyrhiza;* Ty_an=*Typha angustifolia*; Ty_la=*Typha latifolia* Ca_ac = *Carex acutiformis*; Ec_cr=*Echinochloa crus-galli*; Ir_ps=*Iris pseudacorus*; Al_pa = *Alopecurus pratensis*; Ca_se=*Calystegia sepium*; Ly_vi=*Lythrum virgatum*]

Taxon	**Bu_um**	**Ce_de**	**Hy_mo**	**Le_mi**	**Le_tr**	**Sa_na**	**Sp_po**	**Ty_an**	**Ty_la**	**Ca_ac**	**Ec_cr**	**Ir_ps**	**Al_pa**	**Ca_se**	**Ly_vi**
Aedvex	(-)6.0963	(-)32.7069	(-)23.4746	(-)55.0575	(-)19.6958	(-)41.0586	(-)34.3495	(-)14.4852	(-)19.0954	11.8405	(-)5.9299	16.6017			
	p=0.0135000	p=0.0000000	p=0.0000013	p=0.000000	p=0.0000091	p=0.0000000	p=0.0000000	p=0.0001415	p=0.0000125	p=0.0005803	p=0.0148910	p=0.0000462			
Aedcin		(-)15.4365	(-)9.7634	(-)4.8845		(-)26.5510	(-)22.0491			8.7938	(-)8.8025			(-)4.5183	
		p=0.0000855	p=0.0017818	p=0.0271057		p=0.0000003	p=0.0000027			p=0.0030247	p=0.0030103			p=0.0335400	
Aedros				(-)17.9461											5.7163
				p=0.0000228											p=0.0168135
Ochexc			(-)8.2377					(-)6.1311		7.4455					
			p=0.0041055					p=0.0132872		p=0.0063629					
Ochann	(-)27.2667	(-)34.9108	(-)47.6154	(-)24.7676	(-)4.6987	(-)36.1478	(-)40.1551		(-)19.9217	117.2044	(-)20.4100	18.1859	(-)4.8272	(-)22.3906	
	p=0.0000002	p=0.0000000	p=0.0000000	p=0.0000007	p=0.0301917	p=0.0000000	p=0.0000000		p=0.0000081	p=0.0000000	p=0.0000063	p=0.0000201	p=0.0280207	p=0.0000022	
Ochcan	(-)9.0572	(-)8.0753	(-)16.2172	(-)5.3664		(-)9.2768	(-)9.3653	(-)8.6260	(-)7.2598	19.1546		13.4197	(-)7.7501	(-)5.9812	(-)10.16572
	p=0.0026186	p=0.0044900	p=0.0000566	p=0.0205335		p=0.0023226	P=0.0022131	p=0.0033163	p=0.0070552	p=0.0000121		p=0.0002494	p=0.0053739	p=0.0144643	p=0.0014321
Ochcat							(-)8.4570			21.3379					
							p=0.0036388			p=0.0000039					
Ochcas	(-)17.5170	(-)11.7131		(-)26.6073	(-)5.2855	(-)11.3927	(-)13.9755		(-)14.2534	(-)17.4612	9.5858	(-)9.0197	75.2097		4.1627
	p=0.0000286	p=0.0006214		p=0.0000003	p=0.0215095	p=0.0007382	p=0.0001855		p=0.0001601	p=0.0000294	p=0.0019626	p=0.0026729	p=0.0000000		p=0.0413303
Ochsti		(-)16.3155	(-)10.0615	(-)18.6662	(-)8.6254	(-)18.7443	(-)18.9305	(-)6.6159		8.4252		6.1946			
		p=0.0000537	p=0.0015154	p=0.0000156	p=0.0033173	p=0.0000150	p=0.0000136	p=0.0101115		p=0.0037030		p=0.0128188			
Ochrus		(-)5.9259				(-)7.5796	(-)12.9721	(-)8.4653		24.7512				(-)9.5049	
		p=0.0149253				p=0.0059063	p=0.0003486	p=0.0036223		p=0.0000007				p=0.0020509	
Ochref										13.9710					
										p=0.0001860					
Ochfla	(-)10.4130	(-)9.9021	(-)12.0111	-17.8610		(-)10.6664	(-)17.9528		(-)15.7637	6.3820		13.2755	6.3498	(-)13.3632	
	p=0.0012525	p=0.0016524	p=0.0005295	p=0.0000238		p=.0010921	p=0.0000227		p=0.0000719	p=0.0115326		p=0.0002693	p=0.0117439	p=0.0002570	
Ochnig													8.1022		
													p=0.0044238		
Ochdor										(-)7.4036			42.5107		
										p=0.0065126			p=0.0000000		
Coqric		6.6864	9.6381	5.0673	22.7713	6.4938	10.2022		51.2584	(-)6.3239					
		p=0.0097190	p=0.0019074	p=0.0243869	p=0.0000018	p=0.0108292	p=0.0014041		p=0.0000000	p=0.0119167					

Table 5

(continued)

Anomac	8.9987	54.6141	39.8667			85.79544	50.5309	49.4395	8.7762	(-)98.3445	5.8504	(-)20.74967		10.10287	8.4541
	p=0.0027037	p=0.0000000	p=0.0000000			p=0.0000000	p=0.0000000	p=0.0000000	p=0.0030540	p=0.0000000	p=0.0155782	p=0.0000053		p=0.0014818	p=0.0036446
Anocla	7.8702		6.9080	15.2297	13.2979			(-)5.9418	8.4850		(-)8.1538		(-)9.4170		(-)15.80606
	p=0.0050285		p=0.0085851	p=0.0000954	p=0.0002661			p=0.0147912	p=0.0035833		p=0.0042997		p=0.0021515		p=0.0000703
Anomes		5.2951		4.5303	11.0570	8.8465	9.7121	6.5400	10.9502	(-)13.8844		(-)4.987010			
		p=0.0213909		p=0.0333074	p=0.0008845	p=0.0029386	p=0.0018232	p=0.0105520	p=0.0009370	p=0.0001947		p=0.255452			
Anohyr	5.2501	5.1998	6.9957			12.4545		13.0621							
	p=0.0219519	p=0.0225958	p=0.0081742			p=0.0004176		p=0.0003018							
Anoalg	5.4917	3.9350		8.2112	11.5364			6.6301							
	p=0.0191129	p=0.0472980		p=0.0041659	p=0.0006833			p=0.0100310							
Anoatr													22.8075		
													p=0.0000018		
Culmod	6.9152	47.9084	62.2562	44.2330	10.3757	73.7738	53.5835	37.9657	23.7387	(-)44.6800		(-)15.21104	(-)9.0701	12.2682	
	p=0.0085503	p=0.0000000	p=0.0000000	p=0.0000000	p=0.0012781	p=0.0000000	p=0.0000000	p=0.0000000	p=0.0000011	p=0.0000000		p=0.0000963	p=0.0026002	p=0.0004614	
Culpip				7.4189						(-)27.5562	52.6489	(-)14.9850		15.0357	6.9796
				p=0.0064575						p=0.0000002	p=0.0000000	p=0.0001086		p=0.0001057	p=0.0082482
Culter	15.1416	17.2257	23.3352	18.4784		14.4759	11.9327		5.7293				(-)4.468527		(-)5.4402
	p=0.0000999	p=0.0000333	p=0.0000014	p=0.0000172		p=0.0001422	p=0.0005523		p=0.0166891				p=0.0345325		p=0.0196837
Cultor					5.2750										
					p=0.0216394										
Culhor								12.2031			9.8531				10.55501
								p=0.0004777			p=0.0016969				p=0.0011599
Culmor					4.5461				9.6124						
					p=0.0330013				p=0.0019344						
Culann	5.5486			14.5132						8.3626	(-)8.6260	3.9072	(-)36.3026	14.5833	(-)23.9973
	p=0.0185014			p=0.0001394						p=0.0038327	p=0.0033162	p=0.0480865	p=0.0000000	p=0.0001343	p=0.0000010
Uraung						4.6211		9.9543		(-)27.8091	6.3735	(-)14.3112		9.6211	12.0682
						p=0.0315877		p=0.0016062		p=0.0000001	p=0.0115879	p=0.0001552		p=0.0019251	p=0.0005136

DISCUSSION

Our results confirmed some former statements about habitat requirements of the mosquito larvae and revealed the most important indicator variables.

Effect of the shading

Our results about affinity to shaded or opened habitats also fit into the former knowledge. It is known that the light requirement characterizes each mosquito species individually. Two species-groups can be separated: group of sunny-preferent taxa and group of shady-preferent taxa (Joy & Clay, 2002; Tóth, 2007). In our samples the sunny-preferent taxa were typical in habitat-types of herb vegetation (HV) and marshy closed vegetation (MV), shady-preferent taxa were typical in habitat-type of forest vegetation (FV).

Effect of the temperature of the breeding water

Our results showed that the univoltine species related to low water temperature. These species hatch usually in early spring, influence of the low temperature is determinant both in their phaenology and longer breeding time (Becker *et al.*, 2003). Further, same species breeds slowly in low temperature and fast in high temperature (Bayoh & Lindsay, 2003; Barton & Aberton, 2005; Tóth, 2007).

Vegetation of the breeding site as a habitat variable

We stated that occurrences of the mosquito species are related to plant species with similar habitat requirements. Based on this, typical mosquito larvae of permanent waters accompanied by pondweeds and other hydrophytic plant species, whereas typical mosquito larvae of temporary waters occur parallel with plant species typical in humid grasslands, or meso-xerophytic meadows.

Cover of the water surface as a limiting factor

Our results showed that the full-covered (mostly by vegetation, *e.g.* pondweeds, lemnas) water surfaces and the large, deep, billowy water bodies are unsuitable for the majority of the mosquito larvae (mainly for the human-biting species). It caused by the biology of mosquitoes: (1) mosquito larvae accommodated to water-life consequentially, so they get oxygen from the air with their siphon (Becker *et al.*, 2003); (2) mosquito larvae are sensible to water movement, because that balks their respiration and kills them (Tóth, 2007).

Effect of water cover

According to our results the period of the water cover (permanent or temporary) plays the most important role in organization of the mosquito assemblages (Table 2). Separation of the species related to this habitat variable based on the relation to dissolved oxygen and the feeding preferences connecting to that. Hatching of *Aedes* and *Ochlerotatus* species takes place at low dissolved oxygen level (Horsfall *et al.*, 1958; Judson, 1960; Becker, 1989). Whereas, hatching of *Anopheles* species related to high level of dissolved oxygen (Surendran & Ramasamy, 2005; Opoku *et al*., 2007). Caused by these differences *Aedes* and *Ochlerotatus* species related to temporary, *Anopheles* species related to permanent, continuously refreshed breeding waters. The water cover period is also important from the egg laying point of view (Schäfer, 2004). Species related to permanent waters are usually multivoltine, which lay their eggs on the water surface. *Aedes* and *Ochlerotatus* species lay their eggs on dry surfaces (usually on wet soil), breeding of these species related to regularly drying zones of marshy vegetation paches and pits of meteoric water.

Determination of the most influential habitat variable

Results of our study marked the period of the water cover as a basic indicator variable of mosquito larval assemblages (Fig. 2). It based on presumably that the period of water cover determines several other habitat variables, like water transparency, presence/absence of pondweed vegetation and percental cover of the water surface. Influence of these parameters was also confirmed by statistical analyses.

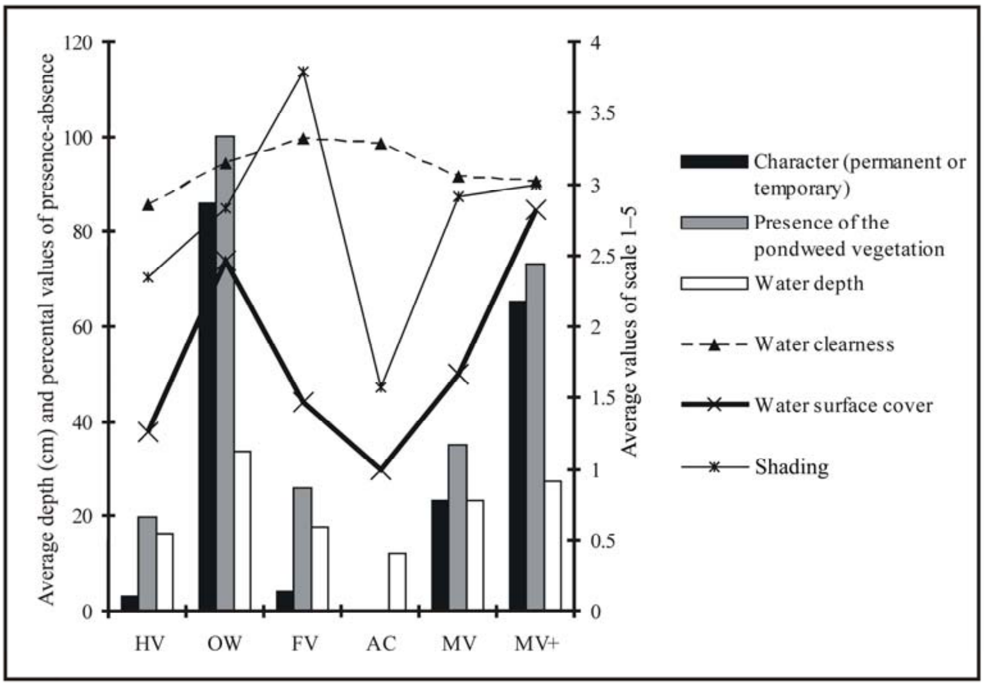

Fig. 2. Basic indicator variables in distribution of the mosquitoe species are related to the regime (permanent or temporary) of the water body [HV: herb vegetation; OW: open water surface; FV: forest vegetation; AC: artificial containers; MV: marshy (reed-bed and sedgy) closed vegetation; MV+: marshy (reed-bed and sedgy) closed vegetation with pondweeds].

Table 6

Significant betas of the multiple regression between densities of the mosquito species and the recorded habitat variables

Species	**Altitude**	**Water depth**	**Water transparency**	**Regime (0/1)**	**Pondweed vegetation**	**Water surface cover**	**Shading**	**Temperature**	**pH**
Aedvex				-0.1046	-0.1172	-0.1012		-0.0043	0.0523
Aedcin			0.0626	-0.0965		-0.0780	-0.0570	0.0041	0.0523
Aedros	-0.0705				-0.0627				0.0519
Ochexc								0.0066	
Ochann	-0.0705		0.1531	-0.0860		-0.1055	0.0864		
Ochcan			0.0935				0.0796	0.0220	0.0601
Ochcat								-0.0637	0.0378
Ochcas	-0.1027			-0.0649	-0.0792	-0.0679		0.0294	0.0653
Ochsti	0.1215		0.0876				0.1108		-0.0126
Ochrus		-0.0704		-0.0538	-0.0713		0.0905		0.0215
Ochref							0.0571	-0.0307	
Ochfla	-0.0801					-0.0688			
Ochnig									
Ochdor	-0.0703						-0.0583	-0.0447	0.0672
Coqric		0.1134	-0.0682	0.1713	0.1236	0.1117		-0.0366	
Anomac	-0.1792	0.0817		0.2380	0.1287	0.0900	-0.0724		0.0239
Anocla	0.1793	0.1336	0.1153	0.1375					-0.0309
Anomes				-0.0837				0.0061	0.0443
Anohyr				-0.0651		-0.0765	0.0586		
Anoalg									
Anoatr							-0.0637	-0.0346	
Culmod	-0.0889			0.0967	0.0949	0.1266			
Culpip						-0.0565			-0.0322
Culter		0.0590		0.0716	0.0600			0.0432	-0.0073
Cultor									
Culhor				-0.0477	-0.0711				0.0677
Culmor	0.0530							-0.0408	
Culmar	-0.0632								
Culann	0.1181						0.1075	0.0079	-0.0071
Uraung	-0.0931							0.0314	0.0293

CONCLUSIONS

Colonization of the mosquito larvae is influenced by the period of the water cover basically. Multicollinearity with the period of the water cover was revealed in connection with some other influental habitat variables: mosquito species related to ephemeral waters are usually related to clear waters, absence of pondweed vegetation and minimal cover of the water surface. On the contrary, mosquito species related to permanent waters are usually related to less water transparency, presence of pondweed vegetation and increased cover of the water surface. Dominat human-biting mosquito species (e.g. *Aedvex, Ochsti, Ochann, Ochcan, Aedros*) usually breed in shallow, quick-warm, regularly drying, clear water bodies with minimal cover of the water surface and without presence of hydrophyta plant species. These habitats occur both in shaded and lightened places.

Our results show that larval habitats of the human-biting mosquitoes separate unequivocally from the habitats irrelevant from biological control point of view. It gives good basis for the more precise mapping and detection of the target areas, and for the environmentally friendly, economically rational BTI-treatments.

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