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DIVERSITY AND ASSOCIATION AMONG *CULICOIDES* (DIPTERA: CERATOPOGONIDAE) FAUNA IN ISRAEL

M. H. BIRLEY[1] and Y. BRAVERMAN[2]

[1]*Department of Medical Entomology, Liverpool School of Tropical Medicine, Pembroke Place, Liverpool L3 5QA, United Kingdom and* [2] *Kimron Veterinary Institute, P.O.Box 12, Bet Dagan, 50250 Israel*

ABSTRACT

The study illuminates the community ecology of *Culicoides* spp. in Israel and aims to improve their control. Light trap data for 34 species from 15 separate locations and years were analysed. The most common species were *C. imicola, C. circumscriptas, C. newsteadi, C. schultzei* group and *C. obsoletus.* Nineteen pairs of positive associations were detected between common and rare species. In larval habitat analysis it was found that mud with medium organic content contained the largest number of species and associations. The following types of association at both the adult and larval level were found: positive association between larvae and negative association between adults, no significant association between adults, but significant association between larvae.

KEY WORDS: Diversity, association, light traps, breeding sites, *Culicoides* spp., Diptera, Ceratopogonidae.

INTRODUCTION

Initial surveys of the *Culicoides* fauna of Israel have been based on random collection and taxonomy (Austen, 1921; Vimmer, 1932; Macfie 1933; Callot *et al.*, 1969). More recently surveys have been conducted in response to outbreaks of epizootic diseases, especially bluetongue (BT), and have included initial attempts to characterise breeding sites and host preferences (Braverman *et al.*, 1971; 1974; 1977; 1981a,b). However, many fundamental ecological parameters remain undetermined and these include density limiting factors and community structure. During surveys conducted since 1967 adults were sampled using light traps which were operated for periods of a year or more at mostly regular but also irregular intervals in fixed locations including cowsheds, stables, sheepfolds and turkey sheds. In addition, larval habitats were sampled by various methods. A large number of *Culicoides* were collected and in tills study the data are analysed for evidence of diversity and association, in space or in time, among the species so obtained.

The objective of the analysis was to obtain a better understanding of the associations and breeding site preferences of those species which are of potential importance for the transmission of BT and Akabane viruses. As BT virus has 24 serotypes, vaccination is not feasible concurrently against more than few types and vector control must be considered (Jones *et al.*, 1981). A knowledge of the breeding site preference of vector species will enable us to target control and minimize the danger to nontarget organisms. *Culicoides imicola*, the principal vector of the above mentioned pathogens in the Mediterranean area and Africa is believed to be a species complex (Wirth & Dyce, 1985). Not all member species may be vectors. One way to identify the species comprising that complex is by identifying the differences in community association of each member species. The end result might be that only one member of the complex will prove to be a vector of BT and Akabane and only against its breeding sites control measures should be directed.

METHOD OF DATA COLLECTION

From 1967 to 1969 the light traps used were mainly of the Du Toit (1944) type, equipped with incandescent bulbs. After 1969 they were mainly fitted with black light fluorescent bulbs (HPW, 125 WE, Philips, Holland). Monks Wood light traps (Service, 1970) equipped with black light fluorescent tubes (TL 6W/05, F6, Philips, Belgium) were used at the Kimron Veterinary Institute, Bet Dagan, since 1980. No change in species composition was noticed by using the various light traps. Traps were hung above farm animals in open-sided, roofed, farm buildings and operated from before sunset until after sunrise. The insects collected were transported to the laboratory where they were sorted by species and sex.

Potential larval habitats were sampled sometimes systematically and sometimes as the opportunity arose between 1968 and 1981. There was probably unconscious bias towards samples expected to contain larvae. As diversity and association indices could be applied only to positive samples producing considerable to large numbers of midges, and not to negative and poor samples, this bias has no meaningful effect on the results. Samples were collected at any season of the year but mainly in the dry season (summer) and from different parts of Israel and Sinai. Substrates were categorised as mud, animal dung or rotten vegetation. The mud was further categorised as poor, medium or rich in organic matter by inspection. Habitats were sampled initially by sugar flotation (Dyce and Murray, 1966), later by emergence trap (Braverman, 1970) and since 1977 by laboratory incubation of standard quantities of substrate in buckets in the insectary at an average temperature of 24.5 to 26.5°C. The subsequent number of individuals emerging from each sample was counted. However, despite the fact that there was no difference between the sample methods and in order to avoid problems of standardisation of sample size and treatment only the presence or absence of species from samples will be considered.

Generally all *Culicoides* were identified but in some cases only a sub-sample could be examined. Identification was based on the taxonomic literature from the Palearactic (Kremer, 1965) and Ethiopian regions (Khamala and Kettle, 1971) with additional support of a slide-mounted reference collection identified by Professor M. Kremer (Strasbourg, France).

The longitude and latitudes of the light trapping localities were: Akko 32°56'N 35°05'E; Bet-Dagan (Kimron Veterinary Institute) 32°00'N 34°49'E; Elon 33°04'N 35°13'E; Gilat 31°19'N 34°39'E; Kabri 33°01'N 35°09'E; Newe Ya'ar (NW YR)

32°42'N 35°11'E and Zetan 31°58'N 34°53'E. The most southern locality, Gilat is located 80 km from and Elon the most northern locality is 118 km from Tel-Aviv.

Samples of preimaginal stages were taken from 119 localities in Israel and Sinai Peninsula extending from E-shira el Gharkana 28°08'N 34°27'E, 438 km south and a site in Mt. Hermon 33°19'N 35°45'E, 165 km north of Tel-Aviv.

The adult and larval sampling area extended from the 1000 mm rainfall at Mt. Hermon to 10 mm at E-shira el Gharkana in Sinai. All vegetation zones (Orni & Efrat, 1973) were sampled, but emphasis was given mainly to the coastal plain with coastal dune and Mediterranean zone lowland vegetation. Second in frequency were the Irano-Turanian zone and the Mediterranean hill vegetation. The remaining Saharo-Arabian zone, Saharo holophytic vegetation and Mediterranean zone high mountain type were sampled sporadically. The most intensive sampling was between the Palearctic and the Palaeoeremic zones (Por, 1975). Less frequently areas belonging to the Palaearctic and patches belonging to Ethiopian fauna were sampled. More detailed information on the zoogeography, geography and climate of the sampled area was given by Braverman *et al.*, 1981.

METHOD OF ANALYSIS

Data was transcribed from the original records in the form of a table for each location and year. Columns indicated total adult females of each species and rows indicated sampling date. Dates spanned approximately the entire year at fairly regular intervals corresponding to about 4 samples per month. The problem was to determine whether these tables contained evidence of species association in time at the sampling location. Many species were rare and observed singly on a small number of occasions. The phototrophic response may differ between species. For these reasons it was considered appropriate to determine pair-wise species association by contingency table analysis rather than product-moment correlation.

The contingency tables were constructed in the usual manner, as illustrated in Table 1. The number of occurrences of species 1 in Table 1 is designated n(ii). The number of joint occurrences of species i and j together is n(ij). The number of samples per year is N. The 2x2 contingency table contains 4 entries: a = n(i-j); b = n(jj)-n(ij); c

TABLE 1. SPECIES ASSOCIATION ANALYSIS BY CONTIGENCY TABLE

		SPECIES i		
		+	–	
SPECIES j	+	a	b	n(jj)
	–	c	d	
		n(ii)		N

= n(ii)-(ij); and d = N+n(ij)-(ii)-n(jj). The chi-squared statistic was calculated from the data in table 1 using the standard formula corrected for continuity. In doubtful cases, where expectations were less than 5 or N was less than 40, the Fisher Exact Test was used (Siegel, 1956; Southwood, 1978). All computations were implemented on a Texas TI-59 programmable calculator and later a PDP II microcomputer.

Significant associations at common levels of probability are determined by the calculated value of chi-squared. The 5%, 1% and .1% probability levels correspond to values of chi-squared of 3.84, 6.63 and 10.83. It must be emphasised that lower values do not indicate a necessary lack of association but merely that the association could have occurred by chance. Further, when several hundred possible pairwise associations are examined then some apparently significant associations at the 5% and 1% level are likely to be false and should be critically examined.

The degree of association may be measured by a number of possible indices (Southwood, 1978). However, we are not aware of previous use of the following index which we refer to as the Bayesian Index of Association (G), i.e.

$$G = \frac{a}{N-d}$$

where there are $\underline{a}$ joint occurrences among 'N' samples in which 'd' samples contain neither species. This is referred to as the Bayesian Index of Association as it measures the probability that if one species is found in a sample then the other species will also be present. This index could also be used to measure association between triplets.

Evidence of adult association in light traps does not, of course, indicate that larvae associate. Larval *Culicoides* are relatively immobile, inhabiting damp semi-aquatic to aquatic breeding sites. In Israel larval habitats are limited and are often temporary or seasonal. They include edges of streams, water reservoirs, rainpools, leaking irrigation pipes, sewage channels from human and animal waste, animal droppings, refuse, rotting vegetation and tree holes (Braverman *et al.*, 1974). Adults are active fliers and seek blood from host animals at intervals of several days. It is not known whether host response is a population regulating factor under intensive livestock rearing schemes. Adult survival is adversely affected by low humidity and high temperatures. However, factors regulating the population density of *Culicoides* in Israel may operate on the longer preimaginal stages in semiaquatic habitats and may include inter- and intra-specific competition. Such competition may lead to partition of the nich in space and time and adaptation to specific abiotic environments (e.g.: temperature, dissolved oxygen or pH requirements). There are three possible forms of association that must be considered at both larval and adult levels: a. no overlap; b. partial overlap and c. total overlap.

At the adult level, where species are found together in the light trap for part of the year, association in time rather than space is observed. No overlap would imply breeding at different times of the year and negative association. Partial overlap would often be observed as positive association. Total overlap would not be distinguished from randomness if the larger niche space were available for the majority of the time.

At the larval level association in space would suggest larval habitats which physically overlap in the same place at the same time while association in time could imply physically separate habitats which become available at the same seasons due to an external driving force such as rainfall or the situation of co-existing competitors.

Diversity, in contrast to association, measures the relative densities of all species in a community. No single index provides a satisfactory measure. Rather, it is preferable to note the total number of species present (S), the total number of individual sampled and to rank the frequency of each species. Community structure may be characterised as dominated by a few species or equitably distributed between species. The Shannon-Weiner function measures degree of equitability (Southwood, 1978).

$$H = -\sum_{i=1}^{S} P_i . \ln P_i$$

where, P_i is the proportion of the ith species, a logarithm of base 2 is sometimes used, and there are S species.

RESULTS

Light trap data from 15 separate locations and years were analysed and the results are presented in Table 2. For each set the diversity of *Culicoides* species is indicated by the number of species observed, the percentage of the four most numerous species and the equitability index (H). Two groups may be distinguished empirically. When H is less than 0.64 the fauna are dominated by a single species, usually *C. imicola* Kieffer, which constitutes more than 84% of the total. When H is greater than 0.64 the principal species constitutes between 28% and 67% of the total and more than one species is present in significant numbers. A single species was dominant in 40% of the data sets.

C. imicola was the most ubiquitous species group while *C. newsteadi* Austen dominated certain more restricted habitats. Elon is near and Kabri is in the banana growing belt of Western Galilee and *C. obsoletus* Meigen breeds there in the rotting stems and trash within the plantations. The high density of *Culicoides* at Kabri, average 822 per night during the year, is due to the extreme seasonal abundance of *C. obsoletus*. At Akko there are believed to be a number of diverse breeding sites and these support a heterogeneous population.

Table 2 also lists the number of significant associations (5% level) detected in each data set. They range from 0 to 9 with no obvious pattern. However, the number of samples at each site was rather small for association analysis and so the light trap data from different locations were pooled and additional miscellaneous samples were added. This could bias the results in favour of certain sites but makes best use of available data. The data then available for association analysis consisted of a total of 668 nights of sampling comprising presence or absence data for a total of 34 species. As 462 pairwise associations are possible some of the apparent significant associations could have occurred by chance. However, some of the rarer species were only observed in one sample and were not always positively identified. There were nine common species found in 9% or more of the samples and these are listed in Table 3. The most common species in order were: *C. imicola* (principal BT vector) 88%; *circumscriptus* Kieffer 38%; *newsteadi* 38%; schultzei group (suspected BT vector) 33%; and *obsoletus*

TABLE 2. DIVERSITY AND ABUNDANCE OF *CULICOIDES* CAUGHT IN LIGHT TRAPS. Abbreviations: DT = DuToit light trap; MW = Monks Wood light trap; WL = white light from incandescent bulb; BL = black light from fluorescent tube in MW and fluorescent bulb in DT; NW YR = Newe Ya'ar

Data set	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Year	1967	1968	1968	1969	1969	1969	1974	1980	1980	1980	1980	1980	1980	1980	1980
Location	Kimron	Kimron	Gilat	Kimron	NW YR	Gilat	Zetan	Elon	Akko	Kabri	Kimron	Kimron	Kimron	Kimron	Tel Aviv
Principal host	Sheep	Sheep	Sheep	Sheep	Cow	Sheep	Turkey	Cow	Horse	Cow	Sheep	Mixed*	Horse	Cow	Zoo
Trap type	DT/WL	DT/WL	DT/WL	DT/WL	DT/WL	DT/WL	DT/BL	DT/BL	DT/BL	DT/BL	MW/BL	MW/BL	MW/BL	MW	DT/BL
No. nights	36	69	30	99	23	40	27	26	39	33	43	70	43	67	42
No. species	8	11	15	11	22	12	8	8	12	10	8	9	9	9	9
No. signif Associations	0	0	2	7	6	6	3	9	6	3	2	4	2	4	1
Mean Culicoides/night	45	51	17	30	62	22	105	102	108	822	19	64	16	16	83
Equitability index	0.19	0.31	1.22	0.46	1.63	1.12	0.64	1.05	1.51	0.58	0.89	0.50	1.22	0.99	1.04
% Frequency of Dominant 4 Species															
circumscriptus	–	–	2	–	–	3	–	10	28	6	1	5	15	3	12
distinctipennis	–	–	–	–	–	–	3	–	–	–	25	–	–	3	–
fascipennis group	–	–	–	–	9	–	–	–	–	–	–	–	–	–	–
imicola	97	94	35	91	5	33	84	27	25	7	67	90	60	55	71
newsteadi	0.5	2	50	–	59	56	8	1	11	–	–	1	16	–	–
obsoletus	0.3	2	–	1	–	–	–	60	–	85	–	–	–	–	–
odiatus	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
punctatus	–	–	–	–	11	–	–	–	–	–	–	–	–	–	–
puncticollis	–	–	–	–	–	–	–	–	–	2	–	–	–	–	8
schultzei group	2	1	6	4	–	5	2	–	–	–	5	1	–	38	5
univittatus	–	–	–	–	–	–	–	–	18	–	–	–	5	–	–

*Mixed = pigs, donkeys and horse

(suspected BT vector) 25%. It should be noted that the relative proportions of these species depends on the relative frequency with which traps were operated in specific habitats.

A total of 111 positive and 7 negative pairwise associations were detected at the 5% level of probability or better. The majority (97) of the positive associations occurred at 0.1% level or greater. However, 71 of these positive associations involved less than 5 joint occurrences and these were excluded from further analysis. Three major groups were then evident: associations among common species; associations among rarer species; and associations between common and rarer species.

The associations between common species occurred mainly at .1% probability level or greater and with Bayesian Index of 0.2 or greater. All the negative associations occurred in this group and enabled the group to be split into two distinct sub-groups. These associations are summarised in Table 3. Positive pairwise associations were found in the following two sub-groups.

1. *C. obsoletus, newsteadi, puncticollis* Becker, *circumscriptus, cataneii* and *univittatus* Vimmer (= *agathensis* Callot, Kremer and Rioux).

2. *C. schultzei* group, *imicola* and *distinctipennis* Austen.

Negative pairwise associations confirmed the two sub-groups as follows:

1. *C. imicola* did not tend to occur with *C. newsteadi, obsoletus* or *univittatus*.

2. *C. schultzei* group did not tend to occur with *C. obsoletus* or univittatus.

3. *C. distinctipennis* did not tend to occur with *C. newsteadi* or *obsoletus*.

In addition, some species were found to commonly occur in pairs but were not significantly associated, i.e. the apparent association could have occurred by chance.

TABLE 3. SIGNIFICANT ASSOCIATIONS AMONG COMMON AND RARER *CULICOIDES* SPECIES CAUGHT IN LIGHT TRAPS. PERCENTAGE OCCURRENCE OF COMMON SPECIES IS LISTED, + POSITIVE ASSOCIATION, - NEGATIVE ASSOCIATION

COMMON SPECIES	*univittatus* 9%	*cataneii* 13%	*circumscriptus* 38%	*distinctipennis* 17%	*imicola* 88%	*newsteadi* 38%	*obsoletus* 25%	*puncticollis* 22%	*schultzei* group 33%	
cataneii	+									
circumscriptus	+	+								
distinctipennis										
imicola	-			+						
newsteadi	+	+	+	-	-					
obsoletus	+	+	+	-	-	+				
puncticollis	+	+	+			+	+			
schultzei group	-			+	+		-			
RARER SPECIES										*punctatus* 2%
badooshensis						+	+			+
coluzzii		+			+		+	+		
fagineus						+	+	+		+
gejgelensis						+				
odiatus										+
pulicaris		+	+			+	+	+		
punctatus						+	+			
semimaculatus			+			+				

1. *C. imicola* was often found with *circumscriptus, cataneii* or *puncticollis*.

2. *C. schultzei* group was often found with *circumscriptus* or *newsteadi*.

Among rarer species there were 3 cases of strong positive association with .1% probability or better and Bayesian index 0.3 or better. The associations were between *C. punctatus* Meigen and *odiatus* Austen, *badooshensis* Khalaf or *fagineus* Edwards.

Nineteen pairs of positive associations were detected between common species and rarer species. See Table 3. It is noteworthy that in the second common sub-group *C. imicola* and *distinctipennis* were not associated with any of the rarer species while *C. schultzei* group was only associated with *coluzzii* Callot and Kremer. In the other common sub-group there were a number of associations especially involving *C. obsoletus* and *newsteadi*.

The larval habitat data were analysed in a similar manner and Table 4 summarises the evidence for diversity and habitat preference. The percentages indicate the proportion of samples from a given substrate in which each species was detected. It may be noted that up to 68% of some substrate samples yielded no *Culicoides*. Mud with medium organic content was sampled most frequently, contained the lowest proportion of empty samples, the largest number of species and the largest number of associations.

TABLE 4. PERCENTAGE OF LARAVAL SUBSTRATES FROM WHICH *CULICOIDES* SPECIES EMERGED. *, **, AND *** ARE 5%, 1% AND .1% SIGNIFICANCE LEVELS FOR CHANGES IN PROPORTION WITH MUD TYPE. +, ++ AND +++ INDICATE INCREASING ORGANIC CONTENT OF MUD

	Substrate					
	Mud				Animal dung	Rotten vegetation
Species	+	++	+++			
begueti	0	0	0		0	3
cataneii	0	7	7	*	2	0
circumscriptus	50	55	55		12	13
coluzzii	8	3	7		0	0
distinctipennis	4	8	3		3	0
fascipennis group	2	0	0		0	0
haranti	0	0	0		0	7
imicola	0	7	17	***	21	0
longipennis	0	1	3		0	0
newsteadi	0	1	0		0	0
obsoletus	1	1	10	**	3	17
puncticollis	20	46	28	***	5	5
schultzei group	16	14	14		3	2
semimaculatus	1	0	0		0	3
univittatus	0	8	0		2	0
% empty samples	41	22	38		68	58
Total samples	98	148	29		66	60
Associations	5	11	1		3	1

Asterisks indicate significant differences, determined by contingency table analysis, in the percentage of a species found in different types of mud. *C. cataneii*, *imicola* and *obsoletus* appeared to prefer mud rich in organic material. *C. puncticollis* appeared to prefer mud of medium organic content. *C. circumscriptus* was ubiquitous. *C. obsoletus* was found in rotten vegetation and mud rich in organic material.

The small number of associations detected in contaminated mud, animal dung and rotten vegetation may be summarised as follows. *C. circumscriptus* associated with *imicola* in organic rich mud, with *obsoletus* or *distinctipennis* in animal dung and with *puncticollis* in rotten vegetation. In addition *C. schultzei* group and *imicola* were associated in animal dung. The pattern of positive pairwise association between larvae in mud which was low or medium in organic material was more complex and is illustrated in Fig. 1.

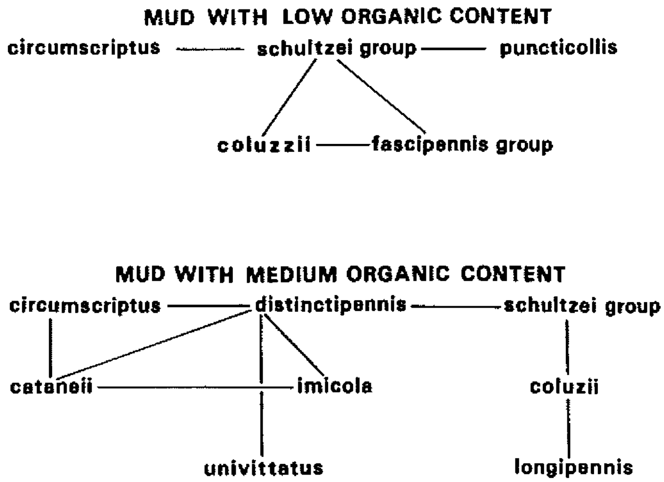

Fig. 1. Significant pairwise associations between larval *Culicoides* species from mud of low and medium organic content.

DISCUSSION

The method of analysis used in this study cannot prove no association. It merely highlights certain possible associations which may be of biological interest. For example, attraction to light traps may depend on many factors and vary between species. The location of the trap in relation to the flight path connecting breeding and feeding sites may be important. Species sampled in the vicinity of a host may not be attracted to that host. The relatively small number of species extracted from larval habitats would suggest either that there are other important larval habitats which were not sampled or that there is an extremely heterogeneous distribution of breeding within available habitats. However, the preference for breeding sites with low or medium organic content is to be expected. Larval *Culicoides* feed on microorganisms and these are most abundant and diverse in relatively uncontaminated water (Patrick, 1962). The knowledge gained on the preference of some *Culicoides* spp. to certain habitats and the species association in breeding sites may enable us to develop control measures specifically against these species.

The results of the association analysis for adults and larvae may now be compared. As adults and larval sampling methods could have different efficiencies it is possible to make relative but not absolute comparisons. A number of conclusions may be drawn. First, there are cases of association at both the adult and larval level such as *C. schultzei* group and *coluzzii, cataneii* and *univittatus, imicola* with *distinctipennis* and *schultzei* group. Some of these associations differ from previous findings, see below.

Second, there are cases of positive association between larvae and negative association between adults such as *C. imicola* and *univittatus* suggesting similar larval niches but different seasonal activity and host preferences (Braverman *et al.*, 1971; Braverman *et al.*, 1981b).

Third, there are cases of no significant association between adults but significant association between larvae such as *C. circumscriptus* with *schultzei* group and *imicola* which suggest that *circumscriptus* has a larger niche. Fourth, there are species which are relatively common as adults but not as larvae such as *C. newsteadi* and vice versa such as *longipennis* Khalaf and *fascipennis* group. The rarity of these species in light traps might be a result of poor attraction to light.

In addition, it may be noted that while *C. imicola* was the most ubiquitous species in light traps, *circumscriptus* was the most ubiquitous species in larval habitats. This would suggest that light traps are undersampling the abundance of *circumscriptus*.

Some adult associations can be explained by known host preferences. For example, ornithophilic species include *distinctipennis* (Braverman *et al.*, 1977), *circumscriptus* (Kitaoka and Morrii, 1964), *cataneii* (Boorman, 1974) and probably *univittatus*. Species with a known preference for large mammals such as cattle and horses include *C. schultzei* group, *C. newsteadi* and *imicola*. The feeding behaviour of *coluzzi* is not known. The apparent association between mammophilic and ornithophilic species in light traps may suggest that the proximity of the host does not have a strong influence on the species sampled and this has previously been noted by Braverman and Rubina (1976).

In a previous study Braverman *et al.*, (1974) examined larval habitats and attempted to characterise the niche space of the species obtained. As a result of that study they expressed confidence in identifying the breeding sites of four ubiquitous species: *C. imicola* (= *pallidipennis*); *C. circumscriptus*; *C. schultzei* group and *C. puncticollis*. They found *C. circumscriptus* and *puncticollis* in similar breeding sites with surface water and rich in organic matter. This association was confirmed in the present study at both adult and larval levels. They found that *C. schultzei* group succeeds *circumscriptus* as a breeding site loses its organic matter over time. This would suggest negative adult association in time and this was confirmed in the present study. They found *imicola* breeding in both kinds of habitats in association with any of the other three species and this was confirmed in the present study. They noted a marked contrast in larval habitats between *C. imicola* (organic rich mud), *distinctipennis* (medium organic mud) and *schultzei* group (poor organic mud). This was not confirmed in the present study. However, observations made following this statistical analysis have tended to confirm the larval habitats suggested by the statistics.

The fact that *C. imicola* was found to breed in medium, organic rich and damp horse manure (Braverman, unpublished) might reflect the plasticity of this species. On the other hand .it might indicate the existence of different members of the *C. imicola* complex.

This study has tried to illuminate the community ecology of *Culicoides* species in Israel using the limited information available. It suggests that adults of 34 species are attracted to a relatively small number of sites containing penned domestic animals and then disperse in search of suitable larval habitats. As Israel is a semiarid country the range of available breeding sites must be very limited except during the wet season, when temperatures are low and little breeding is taking place. The most favourable habitats appear to be mud of low or medium organic content where the common species, except *C. newsteadi*, are found associated. A few rarer species were also present. The breeding sites of most other species have not been ascertained. Yet their association with common species as adults would suggest that they may occupy a small subset of the breeding sites of common species. Further research is required to elucidate the pattern of niche overlap more precisely.

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