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Bionomics of bloodsucking midges (Diptera: Ceratopogonidae: *Culicoides*) on the coastal plain of Georgia, USA

Экология кровососущих мокрецов (Diptera: Ceratopogonidae: *Culicoides*) на равнине у побережья в штате Джорджия, США

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КЛЮЧЕВЫЕ СЛОВА: *Culicoides*, мокрецы, сезонная динамика обилия, видовой состав, новые находки, светоловушка, местообитания личинок, дупла деревьев, экологические факторы, корреляции, регрессионные модели, клещи, мермитиды.

ABSTRACT. Adult *Culicoides* spp. were collected in Bulloch County, Georgia, USA, each week over the 13-month period (June 1995 – June 1996), using CDC miniature light traps baited with 1-octen-3-ol. Collections were made from four contrasting sites of the coastal plain. In addition to light traps, emergence of *Culicoides* was studied from the material collected in four tree holes. A total of 17 species have been collected: *C. alachua* Jamnback & Wirth, *C. arboricola* Root & Hoffman, *C. bickleyi* Wirth & Hubert, *C. biguttatus* (Coquillett), *C. crepuscularis* Malloch, *C. debilipalpis* Lutz, *C. furens* (Poey), *C. haematopotus* Malloch, *C. hinmani* Khalaf, *C. juddi* Cochrane, *C. mulrennani* Beck, *C. nanus* Root & Hoffman, *C. paraensis* (Goeldi), *C. snowi* Wirth & Jones, *C. spinosus* Root & Hoffman, *C. stellifer* (Coquillett), and *C. venustus* Hoffman. Two species, *C. alachua* and *C. juddi*, are recorded for the first time from the state of Georgia, USA. Composition and structure of adult *Culicoides* assemblages assessed for each site. Mite and mermithid parasitism on adult *Culicoides* were considered. Seasonal abundance of different *Culicoides* species was described and correlated with meteorological conditions. Major environmental factors that might influence the abundance of predominant species were analysed using stepwise multiple regression and discussed. Parity of *C. stellifer* females in light trap collections was analysed by the same technique. For each species of *Culicoides*, published and original data were summarized on larval habitats, seasonality and life cycles, biting activity and geographical distribution.

РЕЗЮМЕ. Имаго *Culicoides* spp. учитывались в округе Баллоч (штат Джорджия, США) на 4-х участках равнины у побережья, контрастных по условиям. Сборы проводились еженедельно в течение 13 месяцев (с июня 1995 г. по июнь 1996 г.) с помощью миниатюрных светоловушек типа CDC, в которые добавлялся 1-октен-3-ол в качестве аттрактанта. В дополнение к сборам на свет, изучен вылет *Culicoides* из субстрата, собранного в дуплах 4-х деревьев. Всего было обнаружено 17 видов: *C. alachua* Jamnback & Wirth, *C. arboricola* Root & Hoffman, *C. bickleyi* Wirth & Hubert, *C. biguttatus* (Coquillett), *C. crepuscularis* Malloch, *C. debilipalpis* Lutz, *C. furens* (Poey), *C. haematopotus* Malloch, *C. hinmani* Khalaf, *C. juddi* Cochrane, *C. mulrennani* Beck, *C. nanus* Root & Hoffman, *C. paraensis* (Goeldi), *C. snowi* Wirth & Jones, *C. spinosus* Root & Hoffman, *C. stellifer* (Coquillett) и *C. venustus* Hoffman. Два вида, *C. alachua* и *C. juddi*, впервые отмечаются для штата Джорджия. Для каждого участка изучен видовой состав и структура таксоценозов *Culicoides*. Отмечено паразитирование мермитид и клещей на имаго *Culicoides*. Для различных видов *Culicoides* описана сезонная динамика численности имаго. Установлены корреляции сезонной динамики *Culicoides* с метеорологическими условиями. Возможное влияние важнейших экологических факторов на численность имаго массовых видов проанализировано с использованием пошаговой множественной регрессии. С помощью этого же метода проанализирована доля самок *C. stellifer*, уже откладывавших яйца, в общей чис-

ленности самок этого вида. Для каждого вида *Culicoides* приведён краткий обзор литературных и оригинальных данных по биотопам личинок, сезонности и жизненным циклам, кровососанию и географическому распространению.

Introduction

Bloodsucking midges of the genus *Culicoides* Latreille, 1809 (Diptera: Ceratopogonidae) include over 800 species. Although minute in size (usually no longer than 3 mm), these insects inflict a fierce bite, often resulting in a lesion more painful than that of a mosquito. In addition, many species transmit disease to man and livestock. The most economically significant disease transmitted by *Culicoides* is bluetongue, a viral pathogen which kills or debilitates hundreds of deer, sheep and cattle each year.

Factors currently known to influence population densities of *Culicoides* include breeding habitat, available hosts, and climate. Of these, oviposition sites are of primary importance. *Culicoides* larvae have the potential to develop anywhere their three basic requirements (air, water, and food) are met. Suitable habitats include, first of all, moist soil, rotting wood, cow dung, salt marshes, tree holes, and margins of diverse bodies of water. However, most species display a higher level of specificity for pH, salinity, temperature and light. Larvae commonly fed on detritus, yeast, or algae. Some species are predaceous; they may feed on nematodes, protozoans and other arthropods [Blanton & Wirth, 1979].

Special investigations of larval habitats and development of *Culicoides* in eastern USA are not numerous. An in-depth study of larval habitats in the Tennessee River Valley, USA was conducted in 1953–54 by Snow et al. [1957]. Wirth & Jones [1956] described three new species of *Culicoides* and listed seven more species thought to breed almost exclusively in tree holes. Kardatzke & Rowley [1971] contrasted the larval habitats of nine species in Iowa. They found seven species of *Culicoides* in wooded habitats, five in herbaceous-mud habitats, four in herbaceous-sand habitats and four in alkaline water habitats. Jones [1961b] also reported the larval environments of 29 species. Murphree & Mullen [1991] conducted the most recent in-depth study of *Culicoides* larvae to date, comparing the larval morphology of 49 North American species. To improve laboratory rearing techniques, Linley [1985] compared growth and survival of *C. melleus* (Coquillett, 1901) larvae on four prey organisms, a haline rotifer and three species of nematodes, which varied in size. The effects of nutritional state and light on activity of *C. furens* (Poey, 1853) larvae were examined by Aussel & Linley [1993]. Mullen & Hribar [1988] confirmed that *Culicoides* larvae are good swimmers and described their movements. Magnon et al. [1990] examined the habitat characteristics of various *Culicoides* species from a salt marsh. A significant correlation existed between the presence of *C. hollensis* (Melander & Brues, 1903) larvae, vegetation and presence of potassium in soil.

The research of bionomics of North American *Culicoides* has been primarily directed toward the coastal nuisance species, *C. furens*, *C. hollensis* and *C. melleus*, or the known bluetongue vectors, *C. insignis* Lutz, 1913 and *C. variipennis* (Coquillett, 1901). While various environmental factors (e.g., habitat characteristics or climatic conditions) may be used to predict the presence of *C. variipennis* or *C. furens*, little is known regarding the ecology of most other *Culicoides* species. While, 32 species in North America have the potential to transmit bluetongue and other arboviruses, little effort has been made to understand the ecological factors influencing their habitat selection. Control of *Culicoides* species depends upon a thorough knowledge of their taxonomy, morphology, biology, ecology and the seasonal geographical distribution.

The objectives of this study were to determine species of *Culicoides* occurring on model sites, to examine the population dynamics of adults of these species, and to correlate abundance of adults of different species and meteorological conditions.

Collection sites

Four study sites were chosen within Bulloch County, Georgia, USA. Sites varied with respect to vegetation, wind exposure, larval habitat, proximity to water sources and available hosts.

Site A

Site A (Hodges property, located off Highway 24, East; 32.49°N 81.64°W; 44.9 m above sea level) consisted of a Carolina Bay community with a freshwater pond surrounded by a large cow pasture. The bay covered an area of ca. 2.7 hectare in the southeast corner of the 13.2 hectare pasture. Cypress trees (*Taxodium ascendens* Brongniart, 1833) were located throughout the pond, growing predominantly on the southeast and east perimeter. Sweet gum (*Liquidambar styraciflua* L., 1753) and loblolly pine trees (*Pinus taeda* L., 1753) were also present, though thinly scattered along the borders of the lake. The canopy was sparse. In the pasture, the dominant vegetation was Bermuda grass (*Cynodon dactylon* L., 1805).

Potential larval *Culicoides* breeding areas consisted of cow dung, hoof-prints and muddy shores of the lake. No tree holes were located. The soil class was Pelham loamy sand. Surface layer of soil ranged from dark grey to very dark grey friable loamy sand. Soil was very strongly acidic, low in natural fertility and low in content of organic mater. Soils were poorly drained with slopes ranging from level to two percent. Run off was slow. Water table averaged less than 96.5 cm in depth for two to six months each year.

Potential hosts for blood-feeding *Culicoides* included: cow (*Bos taurus* L., 1758), beaver (*Castor canadensis* Kuhl, 1820), horse (*Equus caballus* L., 1758), raccoon (*Procyon lotor* L., 1758), cotton rat (*Sigmodon hispidus* Say & Ord, 1825) and various bird species including the wood-duck (*Aix sponsa* L., 1758), great blue heron (*Ardea herodias* L., 1758) and killdeer (*Charadrius vociferous* L., 1758).

Light traps were placed along the southern and eastern boundaries of the pond. Wind shelter was minimal.

Site B

Site B (French property, located off Hodges road; 32.54°N 81.77°W; 57.9 m above sea level) consisted of a freshwater pond and uplands covering an area of ca. 9.1 hectares, about 9 km WNW of sites A, C and D. Vegetation bordering the pond was dense and diverse including: black cherry (*Prunus serotina* (Ehrhart) Borkh., 1784), loblolly pine, magnolia (*Magnolia grandiflora* L., 1759), red bay (*Persea borbonia* (L.) Sprengel, 1825), red maple (*Acer rubrum* L., 1753), sweet gum, oak (*Quercus virginiana* L., 1768) and yellow poplar (*Liriodendron tulipifera* L., 1753) trees. Ferns (*Polypodium aureum* (L.) J. Smith, 1841) were also abundant. Most trees were immature and provided little canopy. Undergrowth was substantial.

Possible larval *Culicoides* breeding areas consisted of rotting wood, streams, ditch banks and muddy shores of the pond. No suitable tree holes were located. The soil was classified as Rutledge, poorly drained and sandy, covered with water much of the year. Water table averaged less than 38 cm in depth more than six months each year. Soil surface layer was black to very dark grey sand, 50 to 102 cm thick, and was underlain by dark grey sandy clay loam. Soil was also very strongly acidic, high in organic matter but very low in natural fertility. This site possessed a thicker, darker surface layer, with poorer drainage than site A.

Potential hosts for blood-feeding *Culicoides* included: white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780), grey squirrel (*Sciurus carolinensis* Gmelin, 1788), raccoon, man (*Homo sapiens* L., 1758), cotton rat and various bird species.

Light traps were placed along an overflow stream, below a two metre high dam on the eastern edge of the pond. The dam provided substantial wind shelter.

Site C

Site C (Hagins hardwood forest, located off Burkhalter road; 32.50°N 81.60°W; 44.6 m above sea level) consisted of a mature hardwood forest about 500 m from the Ogeechee River and several freshwater canals. Dominant vegetation included: beech (*Fagus grandifolia* Ehrh., 1788), sweet gum, magnolia, holly (*Ilex* spp.), loblolly pine, and hickory (*Carya* spp.) trees. Ferns were abundant, and the tree canopy was well formed with minimal undergrowth.

Possible breeding areas included: rotting wood, tree holes and neighbouring stream banks. Suitable tree holes were very common. The soil class was Fuquay loamy sand. Soil permeability was moderate to moderately rapid, normally slightly droughted, and consisted of greyish brown to grey loamy sand. Soils were well drained with slopes ranging from two to five percent. The surface layer was thick and extended to a depth of 15 to 20 cm.

Potential hosts for blood-feeding *Culicoides* included: white-tailed deer, grey squirrel, raccoon, cotton rat, eastern wood rat (*Neotoma floridana* Ord, 1818), armadillo (*Dasypus novemcinctus* L., 1758) and various species of birds including wild turkey (*Meleagris gallopavo silvestris* Vieillot, 1817).

Light traps were placed beside selected tree holes throughout the forest. Vegetation provided substantial wind shelter.

Site D

Site D (Hagins ravine, located off Burkhalter road, near Ogeechee River; 32.51°N 81.59°W; 23.0 m above sea level) consisted of a natural ravine running from an underground stream, within a mature hardwood forest about 400 m from the banks of the Ogeechee River. The ravine was ca. 620 m in length and ranged from 3–7 m in depth. Vegetation throughout the ravine was sparse. Dominant vegetation included ferns (*P. aureum*) and holly (*Ilex* spp.) trees. The canopy of the surrounding forest overshadowed the ravine, thus undergrowth was minimal.

No tree holes were located in trees within the ravine; however several tree holes were located along the ravine forest border. Soil was classified as Pelham loamy sand. The surface layer of soil was mottled grey, yellowish brown and grey sandy clay loam, with moderate amounts of organic matter.

Potential hosts for blood-feeding *Culicoides* included: white-tailed deer, grey squirrel, raccoon, eastern wood rat, armadillo, and various species of birds including wild turkey.

Light traps were placed along sides of the ravine. The ravine ditch banks provided excellent wind shelter.

Materials and methods

Light trap collections

Collections were made each week, by CDC (Centers for Disease Control) miniature light traps at sites A and B (June 1995 – June 1996), at site C (July 1995 – June 1996), and at site D (August 1995 – May 1996). As a rule, collections were made once each week using one trap per site. On some nights two or three traps were operated. Each light trap was placed ca. 1 m from the ground and powered with a 6 volt rechargeable battery. Traps were baited with 0.1 ml of 98% 1-octen-3-ol (Aldrich Chemical Co. Inc.). Specimens were collected into a jar containing 70% ethanol. Traps were set about an hour before sunset (near about 19:00) and operated until the following morning (after civil sunrise, about 7:00).

Collections were sorted by species, sex and abdominal pigmentation. Abdominal pigmentation was used to judge reproductive history of females, where red pigmentation indicated parous females with previous ovarian cycles [Dyce, 1969]. The individuals parasitized by nematodes and mites were also noted. The intersexed individuals, expressing the male genitalia and the female mouthparts morphology, were removed and preserved in 70% ethanol.

Sample specimens were dissected and slide-mounted in Euparal (ASCO Laboratories, England). Mounted specimens were examined using the diagnostic characters including the wing length, costal ratio, antennal ratio, palpal ratio, antennal sensory pattern, shape and size of spermathecae, as well as the number and length of tibial spines. The numerical character values from Blanton & Wirth [1979] were used for comparison.

Light trap collections were analyzed with the JMP® 3.02 [SAS Institute Inc., 1994] statistics program (Macintosh II CX personal computer). Collection totals of trap nights were transformed using the formula: $y = \log_{10}(x + 1)$. The Wilcoxon Rank Sums test, the R statistic was applied to determine correlations between species and sites. This test was used to determine correlations between species abundance and environmental (meteorological) parameters. The R^2 value identifies the proportion of the variability of the collection, based on degrees of freedom and number of variables. Variables were considered to be statistically significant at $P \leq 0.05$. Data were analyzed using a stepwise regression model which compared medians of the 49 sample nights. The model determined significant meteorological variables (see below), which influenced trap catch.

The Shannon-Weaver diversity index ($H = -\Sigma\, ith_p \log_e ith_p$), where the ith_p is the relative abundance of each group of organisms in the array of organisms collected from the site, was applied to the collection totals for each site [Lloyd et al., 1968]. Values of H can range from 0 to ~4.6 using the natural log. A value near 0 would indicate that every species in the sample is the same. Conversely, a value near 4.6 would indicate that the number of individuals is evenly distributed between the number of species.

Tree hole samples

Soil samples were taken from four sweet gum tree holes within site C. All tree holes were located near the base of the trees and contained rotting organic matter and mud. The following measurements were taken for each tree hole: tree diameter at the tree hole, area of the opening, and pH of organic material in the hole.

Tree hole A had a diameter of 591.9 cm, an opening area of 84.5 cm^2, and a pH of 9.4. Tree hole B had a diameter of 670.7 cm, an opening area of 518.2 cm^2, and a pH of 9.4. Tree hole C had a diameter of 342.4 cm, an opening area of 61.0 cm^2, and a pH of 8.2. Tree hole D had a diameter of 549.8 cm, an opening area of 13.7 cm^2, and a pH of 9.3.

About 30 cm^3 of debris was scraped from the surface layer (2 cm in depth) of each tree hole and placed within a separate emergence cage. Samples were kept in the laboratory at room temperature (ca. 20°C), moistened with distilled water and monitored daily. Newly-emerging adults were removed and placed in 70% ethanol. Midges were then identified to species and sorted by sex.

The soil sample emergence cages were made as follows: small kitchen funnels, 6.5 cm in diameter were inverted and placed atop 355 ml cups measuring 8 cm in diameter along the upper rim. Each 355 ml cup was covered with a transparent 270 ml cup measuring 9 cm in diameter along the upper rim. Six or eight small holes were punched into the bottom of each 270 ml cup and two holes were made along upper rim of the transparent cup. Paper clips were attached to the transparent cup through holes to form two hook-like structures. Rubber bands were then used to secure the transparent cup to the top of the 355 ml cup. Adult flies emerged into inverted transparent cup on top.

Meteorological observations and other environmental factors

Daily weather readings were obtained from the Georgia Southern University Weather Station and the Georgia Automated Environmental Monitoring Network (Bulloch Co., Sheriffs Dept., Highway 301 North) for Statesboro, Georgia, USA. No weather readings were taken directly from trap locations. Meteorological parameters measured and recorded included: daily rainfall (mm), weekly rainfall (mm), daily air temperature (°C), minimum daily air temperature (°C), maximum air temperature for the trap night (°C), soil temperature (°C averaged over 7 days and over trap night), relative air humidity (%, ratio of amount of water vapour in the air to the maximum amount the air could hold, averaged over trap night), barometric pressure (mm Hg), wind speed (miles per hour), and compass direction of wind.

In addition, lunar phase was considered in the analysis as a parameter that could influence the abundance of *Culicoides* adults in the traps by means of light intensity at night. In the equations, this parameter was used as following: new moon = 1, first and last quarter = 2, and full moon = 3.

The following abbreviations for the parameters are used in the equations:

Max Temp — maximum air temperature for the trap night;
Avg Wk Temp — average weekly air temperature over 7 days prior to trap night;
Soil Temp — soil temperature averaged over trap night;
Avg Wk Soil Temp — average soil temperature over 7 days prior to trap night;
RH — relative air humidity averaged over trap night;
2 Wk Rain — rainfall amount over two weeks prior to trap night;
N — number of individuals of the same species collected 7 days prior to trap night.

Results

A total of 40,449 specimens were collected over the 13-month period using all methods. Seventeen species of *Culicoides* were identified from Bulloch County collection sites (see Tables 1 and 10).

Site A

A mean total of 28,911 individuals were collected by light traps from site A. Eleven species were identified (Table 2). Three species comprised over 99% of the collections: *C. biguttatus* (13%), *C. stellifer* (72%) and *C. venustus* (14%).

Table 1. Monthly light trap collections* of *Culicoides* spp. from Bulloch County, Georgia, USA.
Таблица 1. Сборы *Culicoides* spp. светоловушками по месяцам* в округе Баллоч (штат Джорджия, США).

Culicoides spp.	1995							1996						Totals
	June	July	August	September	October	November	December	January	February	March	April	May	June	
C. alachua Jamnback & Wirth, 1963	–	–	–	–	–	–	–	–	–	–	1.0	–	–	1.0
C. arboricola Root & Hoffman, 1937	–	–	1.3	0.8	6.5	–	–	–	–	–	–	26.0	–	34.7
C. bickleyi Wirth & Hubert, 1962	–	–	–	–	–	–	–	–	–	0.5	4.0	44.5	2.0	51.0
C. biguttatus (Coquillett, 1901)	0.5	1.0	0.9	–	–	–	–	–	–	–	58.0	5,898.0	16.0	5,974.4
C. crepuscularis Malloch, 1915	0.5	–	0.5	1.5	–	–	–	–	–	–	–	–	–	2.5
C. debilipalpis Lutz, 1913	–	3.0	4.5	9.2	–	–	–	–	–	–	–	34.0	–	50.7
C. furens (Poey, 1853)	–	–	–	–	8.0	–	–	–	–	–	–	87.5	44.0	139.5
C. haematopotus Malloch, 1915	9.0	8.3	125.3	91.1	22.5	4.0	–	–	–	–	–	160.5	10.0	430.8
C. hinmani Khalaf, 1952	0.3	6.7	17.8	1.0	–	–	–	–	–	–	–	16.0	12.0	53.8
C. juddi Cochrane, 1973	–	–	0.3	–	–	0.5	–	–	–	–	–	–	–	0.8
C. mulrennani Beck, 1957	1.5	1.0	2.0	32.2	1.5	–	–	–	–	–	–	–	–	38.2
C. nanus Root & Hoffman, 1937	–	0.7	–	0.7	–	–	–	–	–	–	–	2.0	–	3.3
C. paraensis (Goeldi, 1905)	–	–	–	–	–	–	–	–	–	–	–	16.0	8.0	24.0
C. spinosus Root & Hoffman, 1937	–	0.5	–	2.3	2.5	–	–	–	–	–	20.8	694.0	1.0	721.1
C. stellifer (Coquillett, 1901)	129.0	534.8	932.0	1,045.0	134.0	22.0	–	–	–	–	18.5	18,860.0	2,174.0	23,849.0
C. venustus Hoffman, 1925	15.0	140.0	9.2	223.7	100.0	1,290.0	–	–	–	1.5	165.0	1,836.0	432.0	4,212.3.0
Totals	155.8	695.9	1,093.9	1,408.2	275.0	1,316.5	0	0	0	2.0	267.3	2,7675.0	2,699.0	35,588.0
Mean / Week	39.0	174.0	273.5	352.1	68.8	329.1	0	0	0	0.5	66.8	6,918.8	674.8	726.3

* Mean number / trap night (weekly collections averaged over four sites), values summed for each month. Collection totals were calculated by summing the mean collections of species per trap night of each month.

* Среднее число экз. каждого вида на 1 ловушку в течение 1 ночи (еженедельные сборы в среднем по 4 участкам), значения суммированы для каждого месяца. Для расчётов итоговых значений средние значения для каждого вида и месяца были суммированы.

Table 2. Light trap collection totals* of *Culicoides* spp. by sites from Bulloch County, Georgia, USA.
Таблица 2. Суммарные значения сборов *Culicoides* spp. светоловушками по участкам* в округе Баллоч (штат Джорджия, США).

Culicoides spp.	Site				Totals	Mean / Week
	A	B	C	D		
C. alachua	–	1.0	–	–	1.0	0.02
C. arboricola	1.5	16.0	14.8	2.3	34.7	0.7
C. bickleyi	17.5	18.5	15.0	1.0	52.0	1.1
C. biguttatus	3,846.5	676.5	1,311.0	140.5	5,974.5	121.9
C. crepuscularis	–	2.5	–	–	2.5	0.1
C. debilipalpis	–	10.0	32.7	8.5	50.7	1.0
C. furens	115.0	1.5	19.0	4.0	139.5	6.9
C. haematopotus	22.5	73.5	107.3	227.5	430.8	8.8
C. hinmani	0.5	0.5	44.5	8.3	53.8	1.1
C. juddi	0.5	–	0.3	–	0.8	0.0
C. mulrennani	2.5	–	2.7	33	38.2	0.8
C. nanus	–	–	3.3	–	3.3	0.1
C. paraensis	–	–	23.0	1.0	24.0	0.5
C. spinosus	19.8	48.5	591.0	61.8	721.1	14.7
C. stellifer	20,745.0	964.5	442.8	1,706.5	23,858.8	486.9
C. venustus	4,139.0	29.5	26.0	17.0	4,211.5	86.0
Totals	28,910.5	1,832.5	2,633.0	2,211.5	35,587.2	726.3
Mean / week	590.0	374.0	53.7	45.1	726.3	–
Shannon–Weaver diversity index	0.8	1.1	1.4	0.9	0.7	–

* Means of weekly collections (mean number of each species/trap night for each site) were summed to give yearly totals.
* Для расчёта итоговых значений для всего года средние значения еженедельных сборов (среднее число экз. каждого вида на 1 ловушку в течение 1 ночи для каждого участка) были суммированы.

Culicoides biguttatus were collected at site A in low numbers throughout April, June and July (Table 3). The collections peaked dramatically in May with a monthly total of 3,814, which comprised 99% of the total *C. biguttatus* collected from site A. During June, collections dropped substantially and continued at low levels through July.

Meteorological data showed about 18% of the variability in the collection numbers of *C. biguttatus* was explained by the maximum air temperature ($P < 0.04$) and the average relative air humidity ($P < 0.01$) for the trap night. Other variables not measured, accounted for 82% of the variability. With an adjusted R^2 value of 0.176, the following model was constructed for collections of *C. biguttatus* at site A, over the 13-month collection period:

$Y = -0.039 + 0.023$ (Max Temp) $- 0.021$ (RH)

Culicoides venustus were collected at site A from March through November (Table 4). Collections were low during March and April, peaking in May with 43% (4,139 individuals) of the total *C. venustus* collected from site A. Collections fell dramatically in June and remained low through October. A second collection peak occurred in November with 31% (1,287.5 individuals) of the total *C. venustus* collected from site A.

Meteorological data showed about 31% of the variability in the collections of *C. venustus* at site A was most explained by the average relative air humidity ($P < 0.036$) and the maximum air temperature ($P < 0.042$) for the trap night. With an adjusted R^2 value of 0.311, the following model was constructed for collections of *C. venustus* at site A, over the 13-month collection period:

$Y = -1.164 + 0.042$ (Max Temp) $- 0.036$ (RH)

Culicoides stellifer were collected from April through November (Table 5) with a significant peak in May (86% of the total *C. biguttatus*, 17,930 individuals). Collections were moderately high throughout June and July. Collections declined during August, and peaked slightly in September before tapering off in November.

Meteorological data showed about 38% of the variability in collections of *C. stellifer* was most explained by the average relative air humidity ($P < 0.10$) and the average soil temperature ($P < 0.01$) for the trap night. While relative humidity was not significant at the 0.05 level of probability, humidity coupled with average soil temperature (over the trap night) was shown to be significantly correlated with catch totals. With an adjusted R^2 value of 0.378, the following model was constructed for collections of *C. stellifer* at site A, over the 13-month collection period:

$Y = -1.482 + 0.049$ (Soil Temp) $- 0.0159$ (RH)

Monthly collection percentages of parous females of *C. stellifer* from site A are given in Table 6. The stepwise regression model showed that 59% of the variability in collections of *C. stellifer* expressing parity at site A, was significantly correlated with the following conditions of

Table 3. Light trap collection totals* of *Culicoides biguttatus* (Coquillett, 1901) by month and site.
Таблица 3. Сборы *Culicoides biguttatus* (Coquillett, 1901) светоловушками по месяцам и участкам*.

Month	Site			
	A	B	C	D
June 1995	0.5	–	**	**
July 1995	1.0	–	–	**
August 1995	–	0.4	–	0.5
September 1995	–	–	–	–
October 1995	–	–	–	–
November 1995	–	–	–	–
December 1995	–	–	–	–
January 1996	–	–	–	–
February 1996	–	–	–	–
March 1996	–	–	–	–
April 1996	16.0	2.0	13.0	27.0
May 1996	3,814.0	674.0	1,297.0	113.0
June 1996	15.0	–	1.0	**
Totals	3,846.5	676.5	1,311.0	1,706.5

* Means of weekly collections (mean number of the species / trap night for each site) were summed to give monthly and yearly totals.

* Для расчёта итоговых значений для месяцев и всего года, средние значения еженедельных сборов (среднее число экз. данного вида на 1 ловушку в течение 1 ночи для каждого участ–ка) были суммированы.

** No samples taken during these months.

** В течение этих месяцев сборы не проводились.

Table 4. Light trap collection totals* of *Culicoides venustus* Hoffman, 1925 by month and site.
Таблица 4. Сборы *Culicoides venustus* Hoffman, 1925 светоловушками по месяцам и участкам*.

Month	Site			
	A	B	C	D
June 1995	15.5	–	**	**
July 1995	139.0	1.0	–	**
August 1995	5.5	0.5	0.3	2.8
September 1995	222.0	0.5	–	1.2
October 1995	94.0	1.0	2.0	3.0
November 1995	1,287.5	1.5	–	1.0
December 1995	–	–	–	–
January 1996	–	–	–	–
February 1996	–	–	–	–
March 1996	0.5	–	1.0	–
April 1996	148.5	6.0	6.0	4.0
May 1996	1,796.0	18.0	16.0	6.0
June 1996	431.0	1.0	1.0	**
Totals	3,846.5	676.5	1,311.0	1,706.5

*, ** See footnotes to Table 3.

*, ** См. сноски к Табл. 3.

the previous week: relative air humidity averaged over the week prior to the trap night ($P < 0.02$), average weekly air temperature, one week prior to the trap night ($P < 0.01$), total rainfall amount during two weeks prior to the trap night ($P < 0.02$), and the collection totals from this site a week prior to the trap night ($P < 0.02$). With an adjusted R^2 value of 0.594, the following model was constructed for the percent of *C. stellifer* females expressing parity at site A:

Y = 0.178 + 0.006 (RH averaged over week prior to trap night) – 0.007 (Avg Wk Temp) – 0.015 (2 Wk Rain) – 0.021 (N)

Site B

A mean total of 1,832.5 individuals were collected by light traps from site B. Twelve species were identified (Table 2). Two species comprised over 90% of the total collection from site B, *Culicoides biguttatus* (37%) and *C. stellifer* (53%).

Culicoides biguttatus were collected in very low numbers during April (Table 3). The collections peaked during May, with 99% (674 individuals) of the total collection of *C. biguttatus* from site B. This species was collected in very low numbers during August.

Meteorological data showed that about 13% of the variability in collections of *C. biguttatus* at site B were most explained by the average relative air humidity ($P < 0.04$) and the maximum air temperature ($P < 0.05$) of the trap night. With an adjusted R^2 value of 0.13, the following model was constructed for collections of *C. biguttatus* at site B, over the 13-month collection period:

Y = –0.110 + 0.013 (Max Temp) – 0.010 (RH)

Culicoides stellifer were collected from May through November (Table 5). The collections peaked during May with 43% (416.5 individuals) of the total collection of *C. stellifer* from site B. The collections dropped slightly in June and again in July. The collections then remained low but stable through November.

Meteorological data showed that 65% of the variability in collections of *C. stellifer* at site B was most explained by lunar phase ($P < 0.04$), average soil temperature for the trap night ($P < 0.01$) and rainfall amount during two weeks prior to the trap night ($P < 0.03$). With an adjusted R^2 value of 0.652, the following model was constructed for collections of *C. stellifer* at site B, over the 13-month collection period:

Y = –1.957 + 0.046 (Soil Temp) – 0.115 (2 Wk Rain) – 0.259 (lunar phase)

Monthly collection percentages of parous females of *C. stellifer* from site B are given in Table 6. Statistical analysis showed that 40% of the variability in collections of *C. stellifer* expressing parity at site B, was significantly correlated with the amount of rain two weeks prior to the trap night ($P < 0.20$). With an adjusted R^2 value of 0.404, the following model was constructed for the percent of *C. stellifer* females expressing parity at site B:

Y = 0.266 – 0.291 (2 Wk Rain)

Site C

A mean total of 2,633 individuals were collected by light traps from the hardwood forest, site C. Fourteen species were identified (Table 2). Three species comprised over 89% of the total collection from site

Table 5. Light trap collection totals* of *Culicoides stellifer* (Coquillett, 1901) by month and site.
Таблица 5. Сборы *Culicoides stellifer* (Coquillett, 1901) светоловушками по месяцам и участкам*.

Month	Site			
	A	B	C	D
June 1995	100.5	28.5	**	**
July 1995	303.5	230.0	1.3	**
August 1995	56.0	81.5	97.7	232.3
September 1995	211.5	64.5	12.3	189.2
October 1995	47.5	23.0	24.5	9.8
November 1995	19.5	1.5	1.0	–
December 1995	–	–	–	–
January 1996	–	–	–	–
February 1996	–	–	–	–
March 1996	–	–	–	–
April 1996	17.5	–	1.0	–
May 1996	17,930.0	416.5	299.0	214.0
June 1996	2,059.0	109.0	6.0	**
Totals	20,745.0	964.5	442.8	1,706.5

*, ** See footnotes to Table 3.
*, ** См. сноски к Табл. 3.

C: *C. biguttatus* (50%), *C. spinosus* (22%) and *C. stellifer* (17%).

Culicoides biguttatus were collected in low numbers through April (Table 3). During May the collection peaked with 99% (1,297 individuals) of the total *C. biguttatus* collection from site C. Only one specimen was collected in June.

Meteorological data showed that 22% of the variability in the collections of *C. biguttatus* from site C was most explained by the average relative air humidity and the maximum air temperature of the trap night ($P < 0.01$). With an adjusted R^2 value of 0.219 the following model was constructed for collections of *C. biguttatus* at site C, over the 12-month collection period:

Y = –0.177 + 0.022 (Max Temp) – 0.018 (RH)

Culicoides spinosus were collected in low numbers in April (Table 7). Collections peaked in May with 97% (575 individuals) of the total *C. spinosus* collection from site C. A few individuals were also collected in September and October.

Meteorological data showed that 12% of the variability in the collections of *C. spinosus* from site C was most explained by the average relative air humidity for the trap night ($P < 0.09$) and the average soil temperature over 7 days prior to the trap night ($P < 0.05$). While relative humidity was not significant at the 0.05 level of probability, humidity coupled with soil temperature averaged over 7 days, was shown significantly correlated with collection totals ($P < 0.01$). With an adjusted R^2 value of 0.118, the following model was constructed for collections of *C. spinosus* at site C, over the 12-month collection period:

Y = –0.002 + 0.015 (Avg Wk Soil Temp) – 0.011 (RH)

Table 6. Percent of parous females of *Culicoides stellifer* (Coquillett, 1901) in the total number of females of this species collected by light traps each month.
Таблица 6. Доля самок *Culicoides stellifer* (Coquillett, 1901), уже откладывавших яйца, в общей численности самок этого вида, по сборам светоловушками за каждый месяц.

Month	Site			
	A	B	C	D
June 1995	29%	70%	*	*
July 1995	40%	92%	*	*
August 1995	31%	72%	34%	40%
September 1995	46%	73%	52%	61%
October 1995	68%	85%	41%	75%
November 1995	69%	67%	–	–
December 1995	–	–	–	–
January 1996	–	–	–	–
February 1996	–	–	–	–
March 1996	–	–	–	–
April 1996	14%	–	100%	–
May 1996	31%	89%	67%	90%
June 1996	36%	98%	25%	*
Means	40%	81%	53%	67%

* No collections were made during these months.
* В течение этих месяцев сборы не проводились.
– No females of *C. stellifer* were collected, hence no data available.
– Нет данных, т.к. в сборах за эти периоды нет самок *C. stellifer*.

Culicoides stellifer were collected from April through November (Table 5). The collection peaked in May with 68% (299 individuals) of the total collection of *C. stellifer* from site C. Collections dropped dramatically in June and July, however reached a small peak (22%, 98 individuals) in August. Collections remained low from September to November.

Meteorological data showed that 46% of the variability in collection of *C. stellifer* at site C was most explained by the average soil temperature of the trap night ($P < 0.01$) and the total rainfall amount over two weeks prior to the trap night ($P < 0.01$). With an adjusted R^2 value of 0.459, the following model was constructed for collections of *C. stellifer* at site C, over the 12-month collection period:

Y = –1.597 + 0.032 (Soil Temp) – 0.166 (2 Wk Rain)

Monthly collection percentages of parous females of *C. stellifer* from site C are given in Table 6. Statistical analysis showed that 91% of the variability in collections of *C. stellifer* expressing parity at site C, were significantly correlated with the following conditions: lunar phase ($P < 0.02$), average weekly air temperature over 7 days prior to trap night ($P < 0.02$), amount of rainfall during two weeks prior to trap night ($P < 0.02$), and the number of individuals collected 7 days before the trap night ($P < 0.01$). With an adjusted R^2 value of 0.909, the following model was constructed for the percent of *C. stellifer* females expressing parity at site C:

Y = 1.422 + 0.062 (N) – 0.055 (lunar phase) – 0.017 (Avg Wk Temp) – 0.034 (2 Wk Rain)

Table 7. Light trap collection totals* of *Culicoides spinosus* Root & Hoffman, 1937 by month and site.
Таблица 7. Сборы *Culicoides spinosus* Root & Hoffman, 1937 светоловушками по месяцам и участкам*.

Month	Site			
	A	B	C	D
June 1995	–	–	**	**
July 1995	–	0.5	–	**
August 1995	–	–	–	–
September 1995	–	–	1.0	1.3
October 1995	–	–	2.0	0.5
November 1995	–	–	–	–
December 1995	–	–	–	–
January 1996	–	–	–	–
February 1996	–	–	–	–
March 1996	–	–	–	–
April 1996	0.8	2.0	13.0	5.0
May 1996	18.0	46.0	575.0	55.0
June 1996	1.0	–	–	**
Totals	19.8	48.5	591.0	61.8

*, ** See footnotes to Table 3.
*, ** См. сноски к Табл. 3.

Table 8. Light trap collection totals* of *Culicoides haematopotus* Malloch, 1915 by month and site.
Таблица 8. Сборы *Culicoides haematopotus* Malloch, 1915 светоловушками по месяцам и участкам*.

Month	Site			
	A	B	C	D
June 1995	7.5	1.5	**	**
July 1995	0.5	6.5	1.33	**
August 1995	1.5	2.5	3.2	118.2
September 1995	1.5	5.0	7.3	77.3
October 1995	2.5	1.5	7.5	11.0
November 1995	1.0	2.0	1.0	–
December 1995	–	–	–	–
January 1996	–	–	–	–
February 1996	–	–	–	–
March 1996	–	–	–	–
April 1996	–	–	–	–
May 1996	6.0	51.5	82.0	21.0
June 1996	2.0	3.0	5.0	**
Totals	22.5	73.5	107.3	227.5

*, ** See footnotes to Table 3.
*, ** См. сноски к Табл. 3.

Site D

A mean total of 2,212 individuals were collected by light traps from site D. Twelve species were identified (Table 2). Two species comprised over 87% of the collection from site D, *C. haematopotus* (10%) and *C. stellifer* (77%).

Culicoides haematopotus were collected during May, August, September and October (Table 1). A collection peak occurred in August (52%, 118 individuals); however, no samples were taken at this site during June and July.

Meteorological data showed that 47% of the variability in the collections of *C. haematopotus* at site D was most explained by the average soil temperature over 7 days prior to the trap night ($P < 0.01$). With an adjusted R^2 value of 0.468, the following model was constructed for collections *C. haematopotus* at site D, over the 10-month collection period:

Y = –1.509 + 0.028 (Avg Wk Soil Temp)

Culicoides stellifer were collected during May, August, September and October (Table 5). No samples were taken during June or July. The collections were greatest during August (41%, 697 individuals) and September (44%, 757 individuals).

Meteorological data showed that 60% of the variability in the collections of *C. stellifer* at site D was most explained by the average soil temperature over 7 days prior to the trap night ($P < 0.01$) as well as the average wind speed of the trap night ($P < 0.03$). With an adjusted R^2 value of 0.596, the following model was constructed for the collection of *C. stellifer* at site D, over the 10-month collection period:

Y = –0.034 + 0.049 (Avg Wk Soil Temp) – 0.139 (average wind speed of trap night)

Monthly collection percentages of parous females of *C. stellifer* from site D are given in Table 6. Statistical analysis showed that 31% of the variability in the collections of *C. stellifer* expressing parity at site D was significantly correlated with the total rainfall amount during two weeks prior to the trap night ($P < 0.01$). With an adjusted R^2 value of 0.307, the following model was constructed for the percent of *C. stellifer* females expressing parity at site D, over the 10-month collection period:

Y = 0.167 + 2.106 (2 Wk Rain)

Correlations between collection sites and the abundance of *Culicoides* species

Over the 13-month period the following correlations were observed between light trap collections and collection site. There were significant differences in abundance between the collections of *C. biguttatus* at all four site locations ($P < 0.01$). Collections of *C. debilipalpis* at site C were significantly different in abundance from collections of *C. debilipalpis* at site D ($P < 0.01$). Collections of *C. furens* were significantly different at all sites ($P < 0.01$). Collections of *C. haematopotus* were significantly different at all sites ($P < 0.01$). Collections of *C. hinmani* at site C were significantly greater than those at site D ($P < 0.01$). Collections of *C. spinosus* were significantly different at all sites ($P < 0.01$). Collections of *C. stellifer* at site A were significantly greater than collections from site B ($P < 0.02$) and site C ($P < 0.02$). Collections of *C. stellifer* at site B were significantly greater than collections of *C. stellifer* at site C ($P < 0.03$) and site D ($P < 0.02$). Collections of *C. venustus* at site A were significantly greater than collections at site B ($P < 0.02$) and site C ($P < 0.04$).

Table 9. Collections of trombidiid-parasitized adult *Culicoides* spp. by light traps (numbers).
Таблица 9. Имаго *Culicoides* spp., зараженые тромбидиидами, в сборах светоловушками (число экз.).

Site	Month	*C. biguttatus*	*C. crepuscularis*	*C. haematopotus*	*C. stellifer*	*C. venustus*	Totals
A	June 1995	–	–	–	2	1	3
	July 1995	–	–	–	–	1	1
	September 1995	–	–	–	1	–	1
	May 1996	–	–	–	2	1	3
B	June 1995	–	–	1	–	–	1
	July 1995	–	–	1	1	–	2
	August 1995	–	–	1	4	–	5
	September 1995	–	1	1	1	–	3
	October 1995	–	–	–	–	–	–
	May 1996	2	–	–	2	–	4
C	July 1995	–	–	–	1	–	1
	February 1996	–	–	–	1	–	1
	May 1996	2	–	–	–	–	2
D	September 1995	–	–	–	–	–	–
Totals		4	1	4	15	3	27

Mite parasitism

Over the 13-month collection period, 27 adult *Culicoides* were found parasitized by larval trombidiid mites. Mite-parasitized individuals were collected from sites A, B and C (Table 9). Five species were observed to be parasitized by trombidiid mites: *C. biguttatus*, *C. crepuscularis*, *C. haematopotus*, *C. stellifer* and *C. venustus*. Of the 27 parasitized midges collected, eight individuals (30%) were collected at site A, 15 individuals (56%) at site B, and four individuals at site C. All of these specimens were collected in light traps. Additionally, one individual was collected in an emergence trap from tree hole A substrate at site C (see below).

While collection totals were not large enough for statistical analysis, the majority of mite-parasitized individuals were collected during the spring months (Table 9): nine individuals (33%) were collected in May, four in June, four in July, five in August, and four ones in September.

Nematode parasitism

Eleven intersexed adult *Culicoides stellifer* were collected over the 13-month collection period. The genitalia of intersexed individuals were mostly male, while the antennae were mostly female. Mermithid nematodes were found in the abdominal cavity of all the intersexed individuals. Of the eleven adults collected, three were from site A, seven from site B, and one from site D. Parasitized adults of *C. stellifer* were collected in 1995 each month from June through October, and also in May 1996. No other species were collected expressing intersexed morphology.

The morphology of the mouthparts of the intersexed specimens was studied in detail using a scanning electron microscope and published in a separate paper [McKeever et al., 1997], which also included a discussion on the influence of mermithid parasitism on adult morphology of *Culicoides*.

Tree hole samples

Adult *Culicoides* were found developing in each of the four tree holes sampled from site C (Table 10). A total of five species (65 adults) were collected from the miniature emergence traps. The number of species emerging from each tree hole ranged from one (hole B) to four (hole A); see Table 10 for details. Tree holes A and D produced over 89% of the emerging adults, 65% and 25%, respectively.

Emergence of *Culicoides bickleyi* adults began 105 days after the tree hole substrate sample was collected and continued until 110 days (mean = 107.5 days). Emergence of *C. hinmani* began 85 days after the mud was collected and continued until 115 days (mean = 97.5 days). Emergence of *C. nanus* began 35 days after the mud was collected and continued until 110 days (mean = 48 days). Emergence of *C. snowi* began 40 days after the mud was collected and continued until 65 days (mean = 50.5 days). Emergence of *C. stellifer* began 35 days after mud was collected and continued until 100 days (mean = 56.5 days).

Significantly more adults of *C. stellifer* emerged from tree hole A than tree hole B, C or D ($P < 0.01$). Significantly more adults of *C. nanus* emerged from tree hole A than tree hole D ($P < 0.02$).

Discussion

Light trap technique

The majority of the findings in the current study are based upon light trap collections. It is therefore necessary to briefly discuss the advantages and disadvantages of this collection method. Beck [1958], referring often to Preston [1948], described some limitations of light traps. According to these papers and our data, light traps favour nocturnal species, which are attracted to

Table 10. Emergence of adult *Culicoides* spp. (numbers) from site C tree hole debris in 1996.
Таблица 10. Вылет имаго *Culicoides* spp. (число экз.) из субстрата, собранного из дупел деревьев на участке С в 1996 г.

Trees	Month:	February				March						April						May	Totals
	Days until emergence:	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	
A	*C. bickleyi*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	2
	C. hinmani	–	–	–	–	–	–	–	–	–	–	–	2	–	2	–	–	–	4
	C. nanus	2	–	2	3	–	–	1	–	–	–	2	–	–	–	1	1	–	12
	C. stellifer	5	1	4	9	2	–	–	–	–	–	1	2	–	2	–	–	–	25
B	*C. stellifer*	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
C	*C. snowi*	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
	C. stellifer	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
D	*C. hinmani*	–	–	–	–	–	–	–	–	–	–	1	–	1	–	1	–	1	4
	C. nanus	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
	C. snowi	–	1	2	4	–	1	1	–	–	–	–	–	–	–	–	–	–	9
	C. stellifer	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	2
Totals		10	3	8	17	2	1	4	–	–	–	4	4	1	4	3	2	1	65

NOTE. Time period (in days) from date of collection of debris until adult emergence. All substrate samples were collected from tree holes of one of four sweet gum (*Liquidambar styraciflua*) trees on 4 January 1996.

ПРИМЕЧАНИЕ. Указан период времени (в днях) с даты сбора субстрата до вылета имаго. Все пробы субстрата были собраны из дупел 4-х ликвидамбаров (*Liquidambar styraciflua*) 4 января 1996 г.

light and may also show a preference for lower temperatures. Light traps in the same location, ran regularly over a long period of time, will affect the parental population to some degree. Large or small collections are often accidental, coinciding with large emergences and climatic conditions, such as wind. Light trap collections may be useful in estimating population levels. The ratio of two nocturnal species may be compared and dominant species determined. Comparisons may be made between the same species at two different locations. Finally, light trap collections sample only the immediate trapping area, and that collection results should not be extrapolated to wider areas. Despite their many limitations, light traps are still useful tools. They are relatively inexpensive to operate and require little supervision. Information gathered from these collections may be used to determine species present in an area, their numbers and seasonal abundance [Beck, 1958].

Site A

Collection totals of *Culicoides* were consistently the greatest at site A (Table 2). Several environmental factors may have contributed to this finding. Perhaps the most important factor influencing the population level at this site was the relatively stable breeding habitat. The slope from the surrounding pasture toward the lake was very gentle. This allowed the moisture from the bay to cover a larger area, than if the slope were more acute. Unlike the correlations found at the freshwater lake (site B) and the hardwood forest (site C), there were no significant correlations between the collections of *C. stellifer* at this site and the rainfall. Characteristic of the Carolina Bay, fluctuations in the water level were minimal, horizontally less than 3–4 metres over the 13-month period. Hence, the surrounding soil was less affected by the presence or absence of rainfall and developing larvae were less threatened with desiccation.

The daily routine of the cattle probably also affected the breeding habitat, by providing fresh hoof prints near the bay daily. These prints broke through the pasture vegetation and provided access to the underlying mud.

The steady blood-meal supply, which the cattle provided, also probably contributed to the abundance of adults. *Culicoides stellifer* and *C. venustus*, the dominant species from this site, are both thought to feed on mammalian blood; *C. biguttatus* is known to feed on cattle (see below).

In addition, the lack of heavy canopy and woody vegetation exposed this environment to greater levels of sunlight, moonlight and wind. The higher levels of insolation may have directly influenced the relative air humidity, a factor which significantly correlated with collections of the dominant species at this site. Species less tolerant of dry air may find this habitat inhospitable. Higher wind speeds at this location may have been responsible for skewing light trap collections such that smaller species were incapable of directional flight. This may also explain the sporadic large collections of *C. biguttatus* when wind speeds fell below 4 miles per hour (Table 11).

Moonlight was also correlated with collections at this site (Table 12). *C. stellifer* and *C. biguttatus* were more abundant during the last quarter and the new moon, while *C. venustus* was most abundant during the first quarter, last quarter and new moon. These data are contrary to those of Lillie et al. [1988]. In Florida, they reported increased activity of three *Culicoides* species (*C. barbosai* Wirth & Blanton, 1956, *C. floridensis* Beck, 1951 and *C. furens*) during the full moon. However, preference for specific light levels varies with species [Blanton & Wirth, 1979].

Table 11. Summary of environmental factors affecting light trap collections of the four most abundant *Culicoides* species at each of the four sites in Bulloch County, Georgia, USA.
Таблица 11. Факторы внешней среды, оказывающие воздействие на сборы светоловушками 4-х наиболее массовых видов *Culicoides* на каждом из 4-х участков в округе Баллоч (штат Джорджия, США).

Species	Site	Min. mean soil temperature 7 days prior to collection date (°C)[1]	Max. mean wind speed (miles per hour)[2]	Max. mean air humidity (%)[2]	Mean air temperature (°C)		Air temperature (°C)[3]	
					Min[1]	Max[2]	Max	Min
C. biguttatus	A	22.2	3.8	64.6	18.2	26.5	35.0	6.5
	B	26.5	3.8	64.6	24.4	26.5	35.0	6.6
	C	23.8	3.8	64.6	18.2	26.5	35.0	6.5
	D	23.8	3.8	64.6	15.1	26.5	34.7	6.5
C. haematopotus	A	20.1	5.8	88.7	18.2	28.6	34.7	10.1
	B	20.1	5.0	90.3	19.2	28.6	35.0	12.8
	C	21.7	5.8	85.4	17.6	28.6	35.0	5.1
	D	21.7	5.8	85.4	17.6	26.5	35.0	5.1
C. stellifer	A	22.2	4.9	85.4	18.2	26.5	35.0	5.1
	B	24.1	5.8	90.3	21.7	28.7	35.0	12.8
	C	23.8	7.9	84.6	17.6	26.5	35.0	6.5
	D	23.8	5.8	85.4	17.6	28.7	35.0	5.1
C. venustus	A	20.1	7.9	88.7	15.1	28.3	35.0	5.1
	B	20.1	7.9	88.7	15.1	27.3	35.0	5.1
	C	16.0	5.8	87.0	12.3	26.5	35.0	6.6
	D	12.1	7.9	85.4	13.4	28.7	34.7	6.5
Mean		21.4	5.7	81.5	17.4	27.3	34.9	7.0

[1] Mean temperature during the trap night above which ≥ 99% of the mean number/trap night by species were collected from the site.
[2] Mean wind speed, relative air humidity or air temperature (each averaged for the trap night) below which ≥ 99 % of the mean number/trap night by species were collected from the site.
[3] The highest (max.) air temperature reached during the trap night below which and the lowest (min.) air temperature during the trap night above which ≥ 99 % of the mean number/trap night by species were collected from the site.
[1] Средняя температура в течение ночи сбора, выше которой было собрано ≥ 99% от среднего числа экз. данного вида на 1 ловушку в течение ночи для данного участка.
[2] Средняя скорость ветра, относительная влажность или температура воздуха (в среднем в течение ночи сбора), ниже которых было собрано ≥ 99% от среднего числа экз. данного вида на 1 ловушку в течение ночи для данного участка.
[3] Максимальная (max.) и минимальная (min.) температура воздуха в течение ночи, ниже и выше которых, соответственно, было собрано ≥ 99% от среднего числа экз. данного вида на 1 ловушку в течение ночи для данного участка.

While collection totals were very high at this site, the diversity was the lowest (H = 0.8). *Culicoides stellifer* made up over 72% of the total collection from this location. This lack of diversity may be attributed to the lack of variance in breeding habitats and host sources. The pasture was burned annually, which reduced the amount of rotting wood and other decaying organic matter. Also, no tree holes were found suitable for breeding.

Site B

The freshwater lake habitat produced the fewest collection totals of all the collection sites in Bulloch County. *Culicoides stellifer* was the most frequently collected species at this site, followed closely by *C. biguttatus* (Table 2). Both of them are soil-breeding species (see below). Collections of *C. stellifer* were significantly influenced by lunar phase as well as rainfall, while collections of *C. biguttatus* were influenced by air humidity and temperature. This was the only location at which *C. alachua* were collected.

The diversity at site B (H = 1.1) was higher than that of sites A and D (Table 2). While no tree holes were discovered in the immediate vicinity of the trap site, rotting wood and other organic debris were found in abundance. Another factor contributing to the diversity may include higher degree of host diversity. With an increase in woody vegetation, this site was inhabited by a stable population of various birds. Therefore, species such as *C. crepuscularis* and *C. debilipalpis*, both of which are ornithophilic (see below), would find this site more favourable than site A.

Site C

Collection totals from the hardwood forest (site C) were the second largest, however, significantly less than the Carolina Bay (Table 2). The reduction in the collections at this location may be attributed to less favourable breeding sites. The lack of moist soil at this site significantly influenced the abundance levels of *Culicoides*. Unlike site A, *C. stellifer* showed a significant correlation with rainfall at this site, indicating fluctuating moisture levels.

Restricting breeding habitat further, the forest floor was uniformly covered with leaves, many of which were magnolia. While many species of *Culicoides* may be found developing in rotting leaves, it is believed that at this site the moisture levels between leaf layers may be insufficient to support larval development. As a result, the leaves may form a barrier to the soil below. Available habitats may also affect population levels of tree hole breeding species. These species compete for the limited available tree holes. In such tree holes, carrying capacity and predation may limit fecundity.

Wind speed appeared to have less affect on the collections of *C. stellifer* at this site than at the other sites. This is probably due to the abundance of woody vegetation at site C, providing wind shelter. Although wind appeared to have a negative affect on collections of *C. venustus* at this site, totals of this species were too low (Table 4) to draw any conclusions. While collections at this site were often too small for statistical analysis, a trend was apparent between collections of *Culicoides* at this site and the last quarter and new lunar phases (Table 12). Again, these data are contrary to those of Lillie et al. [1988].

The diversity level (H = 1.4) at this site was the highest among the four sites in our study (Table 2). This may be attributed to variability in breeding sites. Although large areas of soil at this site were not available as *Culicoides* larval habitats, tree holes and rotting wood were abundant. Some species, such as *C. stellifer*, are capable of breeding in soil, tree holes or rotting debris, and many species, such as *C. nanus*, are strictly tree hole breeders (see below). Such species may have found this site favourable, and thus increased the diversity.

As noted previously, *Culicoides* diversity is influenced by an increase in host diversity. The stable population of birds at this location would be expected to increase the number of ornithophilic species such as *C. debilipalpis*.

Unlike the other locations, *C. stellifer* was not the dominant species, although it was the most consistently collected species. Collection totals of *C. biguttatus* (Table 3) and *C. spinosus* (Table 7) were greater than that of *C. stellifer* (Table 5). However, *C. stellifer* was less sporadic.

Site D

No collections were made from site D during June–July 1995 and in June 1996. The interpretation of results must be weighed with this knowledge; however, statistical analyses of meteorological conditions of the trap nights provided valuable data. *Culicoides stellifer* was the most frequently collected species. As with site A, collections of *C. stellifer* were not influenced by rainfall. This habitat, fed by an underground stream, remained moist throughout the trapping period. Collections were influenced by the mean weekly soil temperature, as well as wind speed. Collections were found to increase at this site as mean daily wind speed increased. While this correlation is not understood, it may be that adults searching for hosts were trapped within the ravine by the winds.

Table 12. Percentages of collection totals from each of the four sites of the four most abundant *Culicoides* species taken with light traps during the different lunar phases.

Таблица 12. Доля каждого из 4-х наиболее массовых видов *Culicoides* в его общей численности на каждом участке во время различных фаз луны, по сборам светоловушками.

Species	Site	First quarter	Full moon	Last quarter	New moon
C. biguttatus	A	1%	9%	63%	27%
	B	< 1%	< 1%	2%	97%
	C	1%	1%	75%	23%
	D	19%	1%	80%	0%
C. haematopotus	A	7%	11%	38%	44%
	B	7%	7%	18%	67%
	C	2%	4%	48%	45%
	D	4%	16%	55%	25%
C. stellifer	A	1%	7%	49%	44%
	B	11%	14%	25%	50%
	C	2%	6%	51%	41%
	D	1%	11%	40%	48%
C. venustus	A	36%	4%	34%	25%
	B	19%	5%	3%	73%
	C	4%	27%	58%	12%
	D	26%	20%	44%	10%
Mean		8.9%	9.0%	42.7%	39.4%

Caution must be taken when examining the correlations between meteorological events and the collection totals of the present study. While these correlations do provide an adequate basis for site comparison, they provide less useful information regarding the direct affect of climatic factors on flight activity and population levels. Such data could only be best gathered from a study in which many traps were run at each site, over a four to five year period. The increased sample size, as well as the longer study period, would distinguish true correlations from mere coincidence. The present 13-month study only provides trends as to which climatic factors may influence light trap collections in the region.

Parity accounts

Abdominal pigmentation may be used to determine the age and reproductive history of female midges [Dyce, 1969]. While each member of a population expresses some degree of pigmentation [Akey & Barnard, 1983], the process by which this pigmentation is produced, is not understood. In females, the degree of pigmentation increases with each gonotrophic cycle and may be used to estimate age and reproductive history of an individual. Caution must be used however, when applying this information to an entire population. Although parity levels may be used to calculate survivorship, Mullens [1985] warned that many factors influence parity levels within light trap collections.

The study by Akey & Barnard [1983] revealed a higher proportion of gravid *C. variipennis* collected in light traps during the crepuscular period. Nulliparous individuals were collected more during dusk, while a higher proportion of parous females were collected during the nocturnal and dawn hours. Collections were also influenced by lunar phase. Gravid females were collected in higher numbers during full moon, while parous females were collected most during new moon.

The distance of the trap from the breeding habitat is also an important factor. Mullens [1985] conducted a study that showed a significantly higher proportion of nulliparous females as the distance from a breeding habitat in California increased. Higher parity levels in females were found nearer the breeding habitat than further away.

Parity levels of *C. stellifer* collections in Bulloch County were influenced by several meteorological factors including relative air humidity, mean weekly air temperature, rainfall amount, and lunar phase. Of these, the rainfall amount occurring during the exact two weeks before the collections appears to affect the parity level at each site. Lunar phase was only significant at site C. No significant correlations were observed between the proportion of gravid females and meteorological conditions.

Mite parasitism

Few conclusions may be drawn regarding mite parasitism of *Culicoides* in Bulloch County. While only 27 parasitized adult *Culicoides* were captured (Table 9), the proportion of parasitized individuals at the collection sites may be much greater. Possibly, the additional weight of small mites affects flight range and duration. If such an assumption is true, light trap collections would naturally be biased against such individuals. Another factor affecting collections of these individuals is the tendency for the mite to become separated from its host when collected into 70% ethanol.

Of the five species found parasitized by mites (Table 9), *C. stellifer* made up over 55% of the parasitized adults. Collections of parasitized individuals were too small for statistical analysis; however, over 55% of the specimens were collected from the freshwater lake habitat. It is also of interest to note mite parasitism of *C. stellifer* from a tree hole habitat.

Tree hole samples

Culicoides were collected from all tree holes sampled, but holes A and D produced over 89% of the emerging adults (Table 10). Both the tree holes shared a similar pH, around 9.3 or 9.4. The influence of pH on developing larvae is well documented. Smith & Varnell [1967] have shown that many tree hole species in Florida prefer a pH greater than 8.7. While only four tree holes were sampled in Bulloch County, pH did appear to play a role in breeding site selection. Tree hole C, the only tree hole with a pH less than 8.7, produced the fewest adults (Table 10), less than 4% of the total collection. Other characters of tree hole C appeared consistent with the more productive tree holes A and D. Tree hole debris was thick and moist at all these sites; the opening of hole C was substantial (61 cm^2).

Desiccation may have also influenced breeding sites. Tree hole B possessed the largest opening, 670.7 cm^2, thus allowing more wind and sunlight to contact the organic debris. The original samples taken from this tree were dry, with evidence of fungal growth. All other original samples were moist. It was also observed that tree hole B drained rain water faster than the other ones.

Potential disease transmission

Monath [1988] noted that *Culicoides* living in close association with cattle, sheep or deer, have the potential to transmit bluetongue. Five species collected from Bulloch County were listed by Monath as potential bluetongue vectors: *C. debilipalpis*, *C. stellifer*, *C. paraensis*, *C. biguttatus*, and *C. venustus*. It is important to note that the three most abundant species in this study (*C. stellifer*, *C. biguttatus* and *C. venustus*) have the potential to serve as vectors of bluetongue virus, however little research has been conducted to determine vector competency. Mullen et al. [1985] have isolated the virus from *C. debilipalpis*.

Species present: a brief review of original and published data on ecology and distribution of *Culicoides* species

Culicoides alachua Jamnback & Wirth, 1963

While the larval habitat of *C. alachua* is presently unknown, other closely-related species are known to breed in wet leaves, compost, manure with straw and similar moist environments involving decaying organic matter and mud [Jamnback & Wirth, 1963]. In the present study, this species was collected from the freshwater lake environment (site B), an area in which rotting organic debris is abundant.

The seasonal distribution of *C. alachua* has been reported from late January to early August in Florida. In northern Florida, *C. alachua* have been collected from April until August [Blanton & Wirth, 1979]. This species is found in northern Florida, South Carolina and Georgia, USA [Blanton & Wirth, 1979]. During our investigation, a single specimen of *C. alachua* was collected during May. This is the first record of *C. alachua* in the state of Georgia, USA.

Culicoides arboricola Root & Hoffman, 1937

C. arboricola larvae have been found in wet tree holes, wet wood debris, water and moist woody debris [Hair et al., 1966]. Snow et al. [1957] found larvae of this species in water and moist debris in tree cavities in the Tennessee River Valley, and Snow & Pickard [1958] found larvae in tree stumps in Alabama. Tree holes were listed as breeding sites in Texas and Wisconsin by Jones [1961b]. Smith & Varnell [1967] also found *C. arboricola* larvae in Florida tree holes. Adults of this species were collected from all of the Bulloch County collection sites; however no adults were obtained by emergence from tree hole samples.

C. arboricola appears to be mainly ornithophilic [Blanton & Wirth, 1979]. Snow et al. [1957] collected females in the Tennessee Valley from inside chicken sheds during daylight hours. Messersmith [1965] found many engorged females in poultry houses in Virginia. Smith & Varnell [1967] collected this species biting man in Florida. Hair & Turner [1968] found *C. arboricola* feeding on both birds and man. Humphreys & Turner [1973] found this species feeding on rabbits in Virginia.

Jamnback [1965] reported this species feeding year round in the warmer southern states. Beck [1952, 1958] collected this species in Florida, from early February to mid-December, with a population peak in July. In Virginia, Messersmith [1966] found *C. arboricola* present from July to September, with a population peak in August. While rarely collected in Louisiana, Khalaf [1969] found this species present from early April through summer. In our study, *C. arboricola* were collected during May, August, September and October, but was highest in May.

C. arboricola has been found in the eastern USA from Minnesota and Texas to Connecticut and Florida, but is more common in the southern part of its range [Blanton & Wirth, 1979]. This species is apparently widespread throughout Georgia, USA, where it was recorded from 12 counties [Williams, 1955; Ah, 1968], but was not known from Bulloch County.

Culicoides bickleyi Wirth & Hubert, 1962

Larval *C. bickleyi* were reared by Wirth & Hubert [1962] from *Sphagnum* taken from a swamp in Maryland, USA. In 1965, Jamnback reared this species from mud in a small woodland stream in New York State. He also found *C. bickleyi* larvae developing in decaying grasses roots, humus and *Sphagnum* on the margins of a New York swamp. In our study, adults of this species were taken from all sites (Table 2) and also were found breeding in a sweet gum tree hole (Table 11).

Wirth & Hubert [1962] reported this species biting man in West Virginia and Massachusetts. Battle & Turner [1971] suggested that the reduced antennal sensory pattern indicates a preference for mammals. Humphreys & Turner [1973] collected female *C. bickleyi* from goats and turkey in Virginia.

Jamnback [1965] stated that *C. bickleyi* is an early spring species, with peak abundance in June in the northeastern and as early as March in the southern USA. Khalaf [1969] reported that this species reached its population peak in Louisiana, during March and disappeared by the last week in May. Blanton & Wirth [1979] collected *C. bickleyi* in April. During our study, *C. bickleyi* were collected from late March until early June (Table 1), but was highest in number in May.

C. bickleyi is found throughout eastern North America. Ah [1968] collected this species in Georgia, USA from Clarke and Houston counties.

Culicoides biguttatus (Coquillett, 1901)

C. biguttatus larvae have been found in lake margins, pools, streams and moist leaf depressions with moist mud, sand or decaying leaves [Wirth, 1951; Williams, 1955; Murray, 1957; Snow et al., 1957]. Snow et al. [1957] discovered pupae in flooded pools and in recently flooded wooded bottom lands in the Tennessee Valley. In Virginia, Hair et al. [1966] found *C. biguttatus* in shaded streams and pool margins. Gazeau & Messersmith [1970] reported rearing this species from dead leaves and mud in a Maryland swamp. In Iowa, Kardatzke & Rowley [1971] reported *C. biguttatus* breeding in wooded, flowing freshwater habitats. In our study, adults of this species were taken from all sites (Table 2).

Although *C. biguttatus* has been reported biting man in Virginia [Murray 1957], Alabama and Tennessee [Snow & Pickard 1958], Jamnback [1965] states that *C. biguttatus* rarely bites man and that many reports of such may be erroneous. Hair & Turner [1968] classified this species as a general feeder. Hoffman [1925] reported *C. biguttatus* as "bad" on cattle. Pickard & Snow [1955] collected *C. biguttatus* feeding on horses; Downes [1958] found it feeding on horses, cattle and chickens. Other reports of this species biting birds have included Jellison & Philip [1933], Downes [1958] and Judd [1959].

Snow et al. [1957] found this species from June through August in the Tennessee Valley. Murray [1957] reported a population peak in Virginia from mid-May to mid-July. Messersmith [1966] collected *C. biguttatus* in Virginia from mid-April to late July with a population peak in June. Along the Gulf Coast of Louisiana and Mississippi, Khalaf [1969] reported *C. biguttatus* appearing after mid-March, with collections peaking from early April to mid-May and disappearing by late June. In our study, this species first appeared during April and remained present until August (Table 1), but were highest at all four sites in May (Table 3).

C. biguttatus is found throughout eastern North America from Wisconsin to Nova Scotia and south to Louisiana and Florida [Blanton & Wirth, 1979]. This species is apparently widespread throughout Georgia, USA, where it has been recorded from 10 counties [Foote & Pratt, 1954; Ah, 1968], but was not known from Bulloch County.

Culicoides crepuscularis Malloch, 1915

C. crepuscularis breeds in a variety of habitats. Wirth & Bottimer [1956] found *C. crepuscularis* larvae in mud at pond margins, puddles at stock tank overflows and in septic tank effluents. In Bermuda, Williams [1956, 1957] reported this species breeding in marsh habitats with a wide range of salinity. In Tennessee, USA, Snow et al. [1957] found *C. crepuscularis* larvae in a rain-filled roadside ditch, as well as in a seepage ditch with marginal grass. Jamnback [1965] reported this species in New York State breeding in cattle hoof print, stream margins, a lagoon margin, and a marshy drainage ditch. He stated that the larval habitats usually include clayey mud with grass roots and humus. Hair et al. [1966] reported that this species was very abundant in mud near livestock watering troughs and pools in open sunlight with little vegetation. Battle & Turner [1970] reported this species from five breeding sites in North Carolina: mud at a ditch margin, mud at a creek margin, mud at the edge of a hog pond, sandy mud at a river margin, and mud at a lake margin. Kardatzke & Rowley [1971] stated this was the most abundant species in Iowa in flowing freshwater habitats, preferring non-wooded, herbaceous-mud environments. *C. crepuscularis* appears intolerant of shady areas [Blanton & Wirth, 1979]. In the present study, *C. crepuscularis* were found only at site B (Table 2).

Most of host preference reports of *C. crepuscularis* suggest it is ornithophilic. Hoffman [1925] collected *C. crepuscularis* feeding on chickens. Jellison & Philip [1933] and Snow et al. [1957] collected it from bird nests. Snow [1955] reported that *C. crepuscularis* is a nocturnal species, which does not penetrate the forest, preferring the canopy level at the forest edge. Pickard & Snow [1955] reported this species biting man in Tennessee. Edmunds & Keener [1954] reported *C. crepuscularis* biting man in Nebraska, but that it rarely bites man elsewhere. Bennett [1960] and Bennett & Fallis [1960] captured this species biting a variety of birds in Ontario, where it was proven to be an intermediate host of a *Haemoproteus* Kruse, 1890 blood parasite of crows and purple finches. Robinson [1961] collected this species in starling traps and infected it with a filarial parasite of starlings. Messersmith [1965] collected large numbers of engorged females in poultry houses in Virginia.

In Florida, Beck [1958] recorded peak populations of *C. crepuscularis* in March. In Tennessee, Snow et al. [1957] reported a population peak in early June. Jamnback [1965] stated that this species produced more than one generation per year in New York, with highest collection numbers in mid to late summer. Childers & Wingo [1968] hypothesized this species had 3–5 generations per year. They also provided notes on seasonal emergence from breeding sites in central Missouri. In Louisiana, Khalaf [1969] considered *C. crepuscularis* an aestival species, reaching a peak population in March, which it maintained until October. In our study, small numbers of this species were taken during June, August and September 1995 (Table 1).

C. crepuscularis is widely distributed in North America from southern Alaska and Canada to northern Mexico, Florida and Bermuda [Blanton & Wirth, 1979]. This species is apparently widespread throughout Georgia, USA, where it was recorded from 6 counties [Williams, 1955; Ah, 1968], but was not known from Bulloch County.

Culicoides debilipalpis Lutz, 1913

Williams [1964] found *C. debilipalpis* larvae in rotting cocoa pods and bamboo stumps in Trinidad. In Virginia, USA, Messersmith [1964] reared this species from wet debris taken from a tree cavity. Smith [1965] reared *C. debilipalpis* from wet tree and stump holes in Florida. Smith & Varnell [1967] stated a preference for breeding environments with a pH less than 8.7. In our study, *C. debilipalpis* were collected from all sites except site A (Table 2), but no adults emerged from tree hole substrate collected at site C.

C. debilipalpis was collected by Messersmith [1966] from chicken houses in Virginia. This species bites man and horses in South America [Blanton & Wirth, 1979]. In Virginia, Messersmith [1966] collected *C. debilipalpis* from mid-June to early August with a population peak in July. Our collections of this species were during May, July, August and September (Table 1), but were highest in May.

C. debilipalpis is found in the southeastern United States from Maryland and Kentucky to Florida and Louisiana, as well as in Central and South America. Ah [1968] collected *C. debilipalpis* from Clarke County, Georgia, USA.

Culicoides furens (Poey, 1853)

Myers [1935] conducted an in depth study of *C. furens* breeding sites in the Bahamas. He noted that excellent breeding areas include waterlogged sand mixed with humus in mangroves. Hull et al. [1934] collected high numbers of *C. furens* larvae developing near Charleston, South Carolina, near the edge of grassy salt marshes and along wet banks of ditches that were reached by high tides only a few days each month. In Virginia, Hair et al. [1966] found *C. furens* in salt marshes and along ditches with *Spartina* vegetation. *C. furens* were taken from all of the sites in our study (Table 2).

Williams [1962] reported that on St.John Island adult *C. furens* may be carried by wind currents across mountains 1,200 feet high and over a distance of 4 miles. Blanton & Wirth [1979] concluded that while wind-borne *C. furens* may be dispersed 3 to 4 miles, upwind dispersal may be limited to only several hundred yards. Linley & Davies [1971] stated that prevailing winds may be an important factor in control measures of *C. furens*. While records of other coastal species have been reported up to 50 miles from the coast [Hinman, 1932], these occurrences are normally attributed to powerful winds. However, significant collections of *C. furens* were taken in our study sites during May 1996 (Table 1), prior to any strong seasonal storms. It is unlikely that these flies were transported via winds over the 50 mile distance from the nearest coastal habitat. Further research is needed to determine breeding locations of these midges.

In Jamaica, Kettle [1969] reported blood-feeding activity of *C. furens* was crepuscular and nocturnal. He also noted that wind speeds above 3 miles per hour significantly decreased biting rates. Kettle & Linley [1969] reported that this species showed a preference for the legs of humans rather than the arms. Snow & Jones [1958] collected *C. furens* in South Carolina five miles from the nearest brackish water, and biting man during the day. They stated that blood-feeding activity ceased after dark. Hair & Turner [1968] classified *C. furens* as a general feeder in Virginia. Unlike most *Culicoides,* this species freely enters confined areas in search of a blood meal.

Khalaf [1969] considered *C. furens* an aestival species in Louisiana. He reported a population peak in May, which persisted with tide-correlated fluctuations until November. In Florida, Beck [1958] found light trap records from Lee County showed higher population levels from May through July, and in October. This report suggests two generations per year in Florida. Blanton & Wirth [1979] reported high numbers of adult *C. furens* at Vero Beach, Florida, from December through June, and in southern Florida adults are most abundant during winter months. Adults are only common northward from April through September. In our research, adults were collected during May, June and October (Table 1), and peaked during May.

Distribution of *C. furens* is quite extensive. The species is found along Atlantic and Gulf Coasts of the USA from Massachusetts to Florida and Texas, along Caribbean and Atlantic coasts of Mexico, Central America, and West Indies to Brazil, and along the Pacific Coast from Mexico to Ecuador [Blanton & Wirth, 1979]. Ah [1968] collected *C. furens* from three counties in Georgia, USA: Chatham, Glynn, and McIntosh.

Culicoides haematopotus Malloch, 1915

Williams [1955] in Georgia, USA, collected emerging *C. haematopotus* over mud in a cypress slough, at a pond margin, and at the margin of a spring-fed stream. Jones [1961b] reported that this species breeds in most of freshwater-soil habitats. Kardatzke & Rowley [1971] found *C. haematopotus* commonly breeding in wooded flowing freshwater habitats in Iowa. This species was collected from all sites in our study (Table 2).

Snow et al. [1957] stated that *C. haematopotus* are normally nocturnal, preferring tree canopy levels. Snow & Pickard [1954] and Pickard & Snow [1955] reported this species biting man in Tennessee during crepuscular periods in spring and fall months. Wirth & Bottimer [1956] also reported *C. haematopotus* biting man in Texas. However, Snow et al. [1957] stated that this species seldom bites humans in the Tennessee Valley. Hair & Turner [1968] classified *C. haematopotus* as a general feeder.

Collections of *C. haematopotus* are known to occur from spring until fall in many areas [Wirth & Bottimer, 1956; Snow et al., 1957]. Beck [1958] reported a population peak in Jackson County, Florida, from March through July. In Virginia, Messersmith [1966] recorded a population peak in June. Childers & Wingo [1968] noted that *C. haematopotus* produced at least three generations per year in central Missouri. Khalaf [1969] classified *C. haematopotus* as aestival in Louisiana, reaching a population peak in April, which was maintained on a lower fluctuating level until October. In our study, adults of this species occurred from May to November, with two peaks, one in May and one in August (Tables 1 and 8), suggesting at least two generations per year in Georgia, USA.

C. haematopotus is widespread over most of the USA, southern Canada, and northern Mexico [Blanton & Wirth, 1979]. This species is apparently widespread throughout Georgia, USA, where it was recorded from 14 counties [Foote & Pratt, 1954; Williams, 1955; Ah, 1968], but was not known from Bulloch County.

Culicoides hinmani Khalaf, 1952

C. hinmani larvae were taken by Wirth & Bottimer [1956] from an oak tree hole in Texas. Snow et al. [1957] found *C. hinmani* developing in moist tree cavities in Tennessee and reported on associated insect species. Hair et al. [1966] stated that *C. hinmani* is relatively rare in Virginia, preferring dry tree holes. A preference for tree holes with a pH above 8.7 was reported by Smith & Varnell [1967] in Florida. While this species was collected from all sites in our study, most collections were from the hardwood forest, site C. Four adults emerged from debris from tree holes A and D (Table 10), both from a pH greater than 8.7.

Snow [1955] found this species biting during daytime in the tree canopy of a forest of Tennessee (reported as *C. borinqueni*). He reported daily activity beginning at lower levels, and spreading upward along main tree trunks in the upper canopy. Snow et al. [1957] found *C. hinmani* biting man in Tennessee, with activity primarily diurnal and not normally in light trap collections. Hair & Turner [1968] collected *C. hinmani* feeding only on small mammals and man, and no specimens were collected from exposed birds. The National Museum of Natural History (Washington, USA) however, contains *C. hinmani* collected in Minnesota from birds in the tree canopy, in Colorado from a chicken baited trap, and in Athens, Georgia, USA, from a poultry house using a CDC miniature light trap.

In Texas, Wirth & Bottimer [1956] trapped *C. hinmani* from early May to late October in Texas. Messersmith [1965] took this species in Virginia from mid-July to early August, with collections peaking in August. Khalaf [1966] found *C. hinmani* in Louisiana from late April through November. In Florida, Blanton & Wirth [1979] recorded this species from April through December, with peak populations in April and May. In the present study, *C. hinmani* were collected from May until September (Table 1). Two collection peaks were observed, in May and in August, suggesting at least two generations per year in Georgia, USA.

C. hinmani is found throughout the eastern United States from Wyoming to Maryland, south to Colorado, Texas and Florida [Blanton & Wirth, 1979]. Ah [1968] collected this species in Georgia, USA from Clarke and Houston counties.

Culicoides juddi Cochrane, 1973

Females of *C. juddi* lack distinct mandibles. Hence, it is unlikely that blood meals are taken. Khalaf [1969] reported *C. juddi* (misidentified as *C. chiopterus* Meigen, 1830) in October from Louisiana and in May, July and September from Mississippi. Low numbers of this species were collected in our study, from sites A and C (Table 2). Collections were taken during August and November (Table 1). This species was reported from Florida, Louisiana, and to New York. This is the first report of *C. juddi* in Georgia, USA.

Culicoides mulrennani Beck, 1957

Blanton & Wirth [1979] reported *C. mulrennani* biting man during crepuscular hours in West Virginia. In Virginia, Humphreys & Turner [1973] collected this species feeding on goat, rabbit and turkey. In our study, *C. mulrennani* were collected from all sites except site B (Table 2).

Records indicate that *C. mulrennani* is present in Florida and Mississippi throughout April and May; in Virginia, West Virginia and Maryland during July; and in New Jersey during August [Blanton & Wirth, 1979]. This species was collected in the present study from June through October, with a peak in September (Table 1).

C. mulrennani is found throughout the eastern United States from Massachusetts to Mississippi and Florida [Blanton & Wirth, 1979]. Williams [1955] collected this species from Baker County, Georgia, USA.

Culicoides nanus Root & Hoffman, 1937

Wirth & Bottimer [1956] reared adults of *C. nanus* from an oak tree hole in Texas. Snow et al. [1957] reared them from wet tree holes in the Tennessee River Valley. Hair et al. [1966] found low numbers of this species in wet tree holes in Virginia. A preference for habitats with pH greater than 8.7 was reported by Smith & Varnell [1967]. In our study, adult *C. nanus* were collected in low numbers from the hardwood forest, site C (Table 2). Adults of this species were also reared from tree holes A and D (Table 10), both having a pH greater than 8.7.

Williams [1955] collected *C. nanus* no later than in late June in Baker County, Georgia, USA. In Oklahoma, Khalaf collected *C. nanus* from late May to the end of July, however reported it as rare. Messersmith [1966] stated that *C. nanus* comprised only 0.28% of his catches in Virginia, from the first of July to the first of September, but collections were greatest in July. Light trap collections in our study were very low and occurred in May, July and September (Table 1).

C. nanus is found throughout eastern North America from Wisconsin to Ontario, south to Texas and Florida [Blanton & Wirth, 1979]. Ah [1968] collected this species from Clarke County in Georgia, USA.

Culicoides paraensis (Goeldi, 1905)

Snow et al. [1957] and Smith [1965] collected *C. paraensis* larvae from tree hole debris in Florida and Tennessee. In Alabama, Snow & Pickard [1958] found this species developing in the tree wound sap of a white oak. Childer & Wingo [1968] also reported *C. paraensis* larvae in a sap-flow in central Missouri. Varnell [1967] reported that *C. paraensis* prefers tree holes with a pH over 8.7. Adults of this species were collected in our study from the hardwood forest (site C) and the ravine habitat (site D) (Table 2). No adults were reared from the tree hole samples of site C; however, tree holes within this site were the most likely breeding habitat.

Snow [1955] stated that *C. paraensis* was very common in the forest canopy in Tennessee. He also stated that feeding activity increased throughout the daylight hours, peaking at dusk. In South Carolina, Snow & Jones [1958] collected this species in the tree canopy, where it readily bit man. Humphreys & Turner [1973] reported *C. paraensis* feeding on rabbits and galliform birds in Virginia. Beck [1958] stated that *C. paraensis* did not readily come to light traps, like most species.

In Tennessee, Snow [1955] collected this species from April to October. Messersmith [1965] took *C. paraensis* from mid-July through mid-August in Virginia. Khalaf [1966] reported this species present in low numbers from April to November in Louisiana. Collections of *C. paraensis* in our study began in May and ended in June (Table 1).

C. paraensis is found throughout the southeastern United States from Louisiana to Pennsylvania, in Mexico and Central America, and in South America. The species also found in the West Indies [Blanton & Wirth, 1979]. *C. paraensis* is widespread throughout Georgia, USA; Ah [1968] collected it from eight counties other than Bulloch County.

Culicoides snowi Wirth & Jones, 1956

Wirth & Jones [1956] reared *C. snowi* larvae from debris in moist tree holes in Virginia. Wirth & Hubert [1962] found this species developing in tree holes in Alabama, Virginia and Tennessee. They also found larvae in oozing sap of a tree wound in Mississippi. Hair et al. [1966] reported *C. snowi* breeding in a stump hole in Virginia. The species was also reported by Smith & Varnell [1967] developing in Florida tree holes. No adults of *C. snowi* were collected in light traps in our study. However, adults were reared from the tree holes C and D in the hardwood forest, site C (Table 10).

Wirth & Hubert [1962] stated that *C. snowi* readily bites man, but is rare in light traps. Therefore it is hard to estimate seasonal population densities. Although Battle & Turner [1971] reported *C. snowi* as an early spring species, Blanton & Wirth [1979] cited records in October, November and March through May.

C. snowi is found from Illinois to Quebec, south to Mississippi and Florida [Blanton & Wirth, 1979]. Ah [1968] collected this species only from Clarke County in Georgia, USA.

Culicoides spinosus Root & Hoffman, 1937

Snow et al. [1957] collected *C. spinosus* larvae in the Tennessee Valley from a reservoir margin, from a rain pool on a mud flat, and from an overflow area of a mountain stream. Battle & Turner [1970] found this species in North Carolina, developing in mud at a stream margin, mud at the edge of a creek, and mud from the overflow of a small pond. *C. spinosus* was collected from all collection sites in our study (Table 2).

Snow [1955] reported *C. spinosus* biting man during daylight hours, especially in crepuscular periods, in the Tennessee bottom lands. He also reported a preference of this species for canopy levels. Jamnback [1965] suggested that the sensillar pattern of this species may indicate a preference for mammals. Humphreys & Turner [1973] collected *C. spinosus* feeding on goats, rabbits and galliform birds in Virginia. This species was also recorded in our study as biting man at dusk, in the freshwater lake habitat, site C.

Jones [1961b] in Wisconsin suggested this species may have two generations per year in the north. Jamnback [1965] stated that this species most likely overwinters in the larval stage in New York state. In Virginia, Messersmith [1966] collected adults from April through August with a population peak in June. In Louisiana, Khalaf [1969] classified *C. spinosus* as "pseudovernal", with higher populations in April, May and October. This species was collected in our study from April through October (Table 1), and numbers were the highest at all four sites in May (Table 7).

C. spinosus is found throughout eastern North America, from Wisconsin to Nova Scotia, south to Louisiana and Florida [Blanton & Wirth, 1979]. Ah [1968] collected this species from six counties of Georgia, USA.

Culicoides stellifer (Coquillett, 1901)

Williams [1955] collected *C. stellifer* in Georgia, USA from emergence cages over moist soil of a cypress slough, a wooded bottom fed by springs, and soil beneath weeds at the margin of a pond. In Virginia, Murray [1957] collected this species along the shallow shady area of a stream edge, which contained decaying leaves. Snow et al. [1957] found pupae in grassy margins of a reservoir and in a rain pool on a mudflat in the Tennessee River Valley. Battle & Turner [1970] reared *C. stellifer* from sites in North Carolina, including mud from a stream margin, overflow from a small pond, mud in a marsh, and mud at a lake margin. Adult *C. stellifer* were collected from all the sites in our study (Table 2). They were also reared from organic debris collected from all studied tree holes in the hardwood forest, site C (Table 10).

Humphreys & Turner [1973] reported this species feeding on turkey in Virginia. Pickard & Snow [1955] reported *C. stellifer* biting man during daylight in forested areas of Tennessee, however later they stated that they had misidentified *C. paraensis* as *C. stellifer* [Snow et al., 1957]. There are currently no records of *C. stellifer* biting man.

C. stellifer was noted by Foote & Pratt [1954] as one of the most common species in the eastern United States. Pickard & Snow [1955] collected this species in Tennessee from April until September with a population peak in May. In Texas, Wirth & Bottimer [1956] also reported peaks in April and May, with another peak in August. In Virginia, Murray [1957] found peaks in June and July. Khalaf [1969] trapped *C. stellifer* in Louisiana from April through November with peaks in May and July. This species was collected in our study from April through November (Table 1), with peaks mostly in May, but also in July–September (Table 5).

C. stellifer is found in North America from Montana and Nova Scotia, south to California and Florida [Blanton & Wirth, 1979]. The species is widespread throughout Georgia, USA, where it was recorded from 12 counties [Foote & Pratt, 1954; Williams, 1955; Ah, 1968], but was not known from Bulloch County.

Culicoides venustus Hoffman, 1925

C. venustus pupae were collected by Snow et al. [1957] from sedges at the margin of a stream entering a reservoir in Georgia, USA. Hair et al. [1966] found this species in a stream margin polluted with feces, near a hog lot in Virginia. Kardatzke & Rowley [1971] reported *C. venustus* breeding on sandbars along creeks in wooded ravines in Iowa. Blanton & Wirth [1979] stated that *C. venustus* are commonly found in wet pastures breeding in muddy hoof prints of livestock. This species was collected from all sites in our study (Table 2). However, the Carolina Bay site (site A) dominated in the collection totals.

While no reports of *C. venustus* biting man are known, Jamnback [1965] states that its well-developed mouthparts and reduced antennal sensoria indicate that *C. venustus* most likely feeds on mammalian blood.

Adult *C. venustus* were collected by Williams [1955] in Georgia, USA during October and November, however, no adults were collected during August or September. Snow et al. [1957] reported collections of this species in the Tennessee River Valley from early spring to fall, with a population peak in mid-June. Jamnback [1965] found *C. venustus* present in low numbers throughout the summer in New York. In Virginia, Messersmith [1965] collected adults from April to September, with a population peak in May. In Louisiana, three peaks were reported by Khalaf [1969]: April, June and a smaller one in late July. Blanton & Wirth [1979] noted that this species is most abundant in April and May, persisting until October. *C. venustus* was collected in this study from late March until mid-November (Tables 1 and 4), and collections peaked at all sites in May.

C. venustus is found throughout eastern North America, from Wisconsin to Nova Scotia, south to Louisiana and Florida [Blanton & Wirth, 1979]. The species is widespread throughout Georgia, USA, where it was recorded from 9 counties [Williams, 1955; Ah, 1968], but was not known from Bulloch County.

In conclusion, it is our hope that the information summarized regarding the life-cycle and biology of *Culicoides* will be of value to reduce the threat of these potential disease vectors upon the health of man and livestock.

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