

HABITAT AND TEMPORAL PARTITIONING OF TREE HOLE *CULICOIDES* (DIPTERA: CERATOPOGONIDAE)

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ABSTRACT. Spring emergence patterns of tree hole *Culicoides* were examined at 11 geographic locations. Habitat selection was one mechanism of partitioning used by *Culicoides*. One group (3 species) occupied tree holes with standing water (wet), while the other (7 species) inhabited tree holes without standing water (dry). The wet tree hole species had sustained emergence patterns, emergence maintained over several consecutive weeks. The dry tree hole species had phasic or biphasic emergence lasting fewer days or occurring as 2 short periods. In both dry and wet habitats, species emerged in a temporal sequence. This temporal sequence was disrupted if a species occupied a type of tree hole (wet/dry) from which it did not normally occur.

INTRODUCTION

Sympatric members of similar species, guilds (Root 1967), which use similar trophic strategies, should deviate in some aspect of their life history (Schoener 1974). This divergence could be multidimensional and involve habitat selection, food utilization or temporal separation (Pianka 1969). Our study of temporal and spatial resource partitioning focuses on 10 *Culicoides* (Diptera: Ceratopogonidae) species which use tree holes, a category of phytotelmata (Frank and Lounibos 1983), for development of immatures.

MATERIALS AND METHODS

Samples (standing water and/or moist organic matter) were collected from 176 tree holes which supported *Culicoides*. The entire contents of each tree hole were removed to Mason jars for transport. In the laboratory, tree hole material was placed in Styrofoam cups and covered with petri dish lids. The samples were monitored daily for emergence of adults. Original consistency of sample material was maintained by periodic addition of distilled water. Following emergence, adults were aspirated into 70% ethanol and mounted on slides (Wirth and Marston 1968) for identification (Blanton and Wirth 1979, Wirth et al. 1985).

Collections were made prior to spring emergence between January and April. Five primary sample locations (samples > 20) were examined. These locations (number of tree holes) were: Liberty Co., FL (22), Fayette Co., GA (30), Mississippi Co., MO (24), Nemaha Co., NE (28), and Brown Co., NE (48). Six secondary locations (samples < 20) were also inspected: Coffee Co.,

TN (8), Grundy Co., TN (2), Barry Co., MO (4), Cape Girardeau Co., MO (2), Montgomery Co., MO (3), and Osage Co., MO (5).

RESULTS

Tree hole *Culicoides* collected in our study occupied 2 basic habitat types. Dry tree holes contain moist organic matter while wet tree holes support standing water (Snow 1949,² Pappas and Pappas 1990). Prior to analyzing emergence pattern and sequence, we categorized habitat preference to ascertain the optimal habitat for each species. Optimal habitat was defined in 2 ways: 1) the tree hole type (wet/dry) with the greatest average number of the species/tree hole, and 2) the tree hole type (wet/dry) supporting the highest percentage of the species.

The dry tree hole habitat was optimal for 7 of the species in our study (Fig. 1). Three species (*Culicoides hinmani* Khalaf, *C. footei* Wirth and Jones, and *C. elemae* Pappas and Pappas) were collected exclusively from dry tree holes. Four species were collected from both habitats but emerged in higher numbers from the dry tree holes. These species were *C. snowi* Wirth and Jones, *C. lahillei* (Iches), *C. nanus* Root and Hoffman, and *C. paraensis* (Goeldi). The wet tree hole habitat was optimal for 3 species. *Culicoides guttipennis* (Coquillett) was collected almost exclusively from the wet habitat. *Culicoides villosipennis* Root and Hoffman and *C. arboricola* Root and Hoffman occurred in both habitats but more specimens/tree hole were taken from the wet tree holes.

We selected the spring emergence pattern of adult *Culicoides* from the Brown Co., NE, site (Fig. 2) as a model for comparison with other collections. This site produced the largest number of individual specimens (575) and species (9) from any collection site examined. Figure 2 does not show *C. arboricola* as only one specimen was collected at Brown Co., NE, or *C. lahillei* which was not found at this site.

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² Snow, W. E. 1949. The arthropods of wet tree holes. Ph.D. thesis. University of Illinois, Urbana, IL, 235 p.

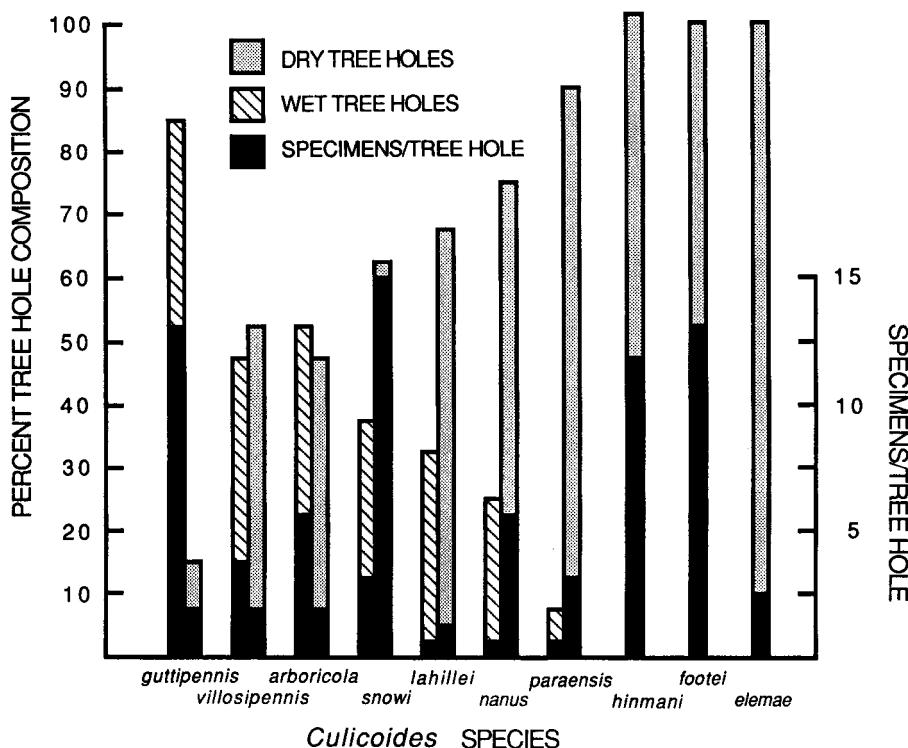


Fig. 1. Habitat and abundance of tree hole *Culicoides* taken from 176 wet and dry tree holes.

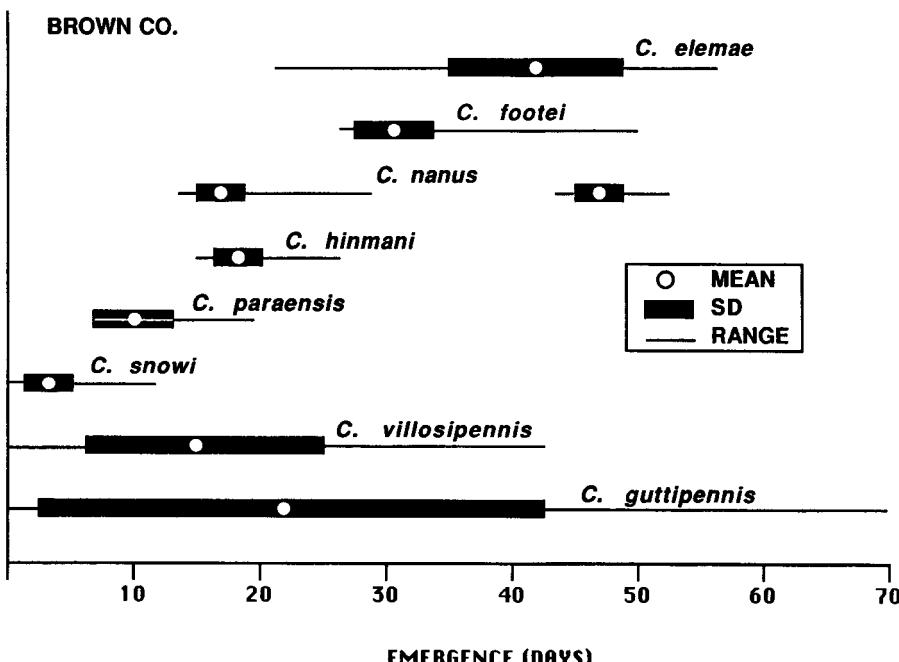


Fig. 2. Spring emergence pattern of tree hole *Culicoides* collected from Brown Co., NE. The emergence date of each species is relative to *C. guttipennis*.

Three types of emergence patterns were detected in the Brown Co., NE, collection (Fig. 2). *Culicoides guttipennis* and *C. villospennis*, wet tree hole species, had sustained emergence patterns lasting several consecutive weeks. *Culicoides elemae*, a species optimally emerging from dry tree holes, had a similar pattern of emergence. These 3 species are part of the *guttipennis* species group (Wirth and Blanton 1967). Four species (e.g., *C. snowi*) had phasic patterns with adults emerging in comparatively shorter time. *Culicoides nanus* exemplified the third emergence pattern which was characterized as biphasic, emerging early with *C. guttipennis*, *C. snowi*, *C. paraensis*, *C. hinmani* and *C. villospennis*, and later with *C. footei* and *C. elemae*.

For the emergence sequence, the initial emergence date of each species in Fig. 2 is relative to *C. guttipennis*, the first species to emerge. Emergence of the 2 wet tree hole species, *C. guttipennis* and *C. villospennis*, overlapped. Of the dry tree hole species, *C. snowi* emerged first followed by *C. paraensis*. Next in sequence was *C. hinmani* which emerged at the same time as the first peak of *C. nanus*. *Culicoides footei* followed the first emergence period of *C. nanus*. *Culicoides elemae* had a peak in emergence following that of *C. footei*.

When *C. guttipennis* was collected from dry tree holes, its emergence was delayed. From the Brown Co., NE, site, 6% of the total *C. guttipennis* specimens came from dry tree holes and began emerging 37 days after the initial emergence from wet tree holes.

In comparing other collection sites to the model developed from Brown Co., NE, similar relationships were observed in both emergence pattern and sequence. *Culicoides guttipennis* was the first to emerge at all primary and secondary collection sites. When present (Missouri and Florida primary samples), *C. arboricola* began a sustained emergence pattern slightly before *C. villospennis* although their standard deviations overlapped considerably. In the Nemaha Co., NE, collection, both *C. arboricola* (3 specimens) and *C. villospennis* (2 specimens) emerged from dry tree holes after the occurrence of *C. guttipennis* from wet tree holes. The emergence relationships demonstrated in the model for *C. paraensis*, *C. nanus*, *C. hinmani* and *C. footei* held in the other 4 primary sample areas. *Culicoides lahillei*, which was collected only from the Florida and Georgia primary sample locations, emerged after *C. paraensis* and before *C. nanus*. In 2 of the primary sample areas, Missouri (4 specimens) and Georgia (1 specimen), *C. snowi* emerged out of sequence, occurring after *C. paraensis*.

We also examined the emergence sequence of species from individual tree holes (Table 1).

This table shows how many times a species occurred with each of the other species and of these times how often their association had the same emergence relationship as our model (see above and Fig. 2). For example, *C. guttipennis* occurred with *C. villospennis* 6 times, and 5 of the 6 times both species emerged at approximately the same time.

For the majority of associations, the relationships seen in Fig. 2 were maintained when examining individual tree holes (Table 1), although there were differences. For example, each time that *C. guttipennis* occurred in a dry tree hole with either *C. paraensis* or *C. hinmani*, *Culicoides guttipennis* emerged much later, relative to these species, than it did from a wet tree hole. Those differences seen in Table 1 occurred primarily when a species occurred outside of its optimal habitat as defined in Fig. 1.

DISCUSSION

One mechanism facilitating habitat partitioning in *Culicoides* may involve developmental and overwintering strategies, of which little is known. Some observations may be relevant in developing hypotheses concerning the emergence patterns of tree hole *Culicoides*. *Culicoides guttipennis* overwinters, at least partially, as larvae. We have collected this species in the 4th instar larval stage in late winter from tree holes while ice was still present. Hair et al. (1966) found *C. guttipennis* at temperatures as low as 2.7°C. We have also noted that the larvae of *C. snowi* and *C. paraensis*, which emerge first in the spring, are present in tree hole samples when initially brought into the laboratory. These 2 species have been collected in early spring by other investigators (Battle and Turner 1971, Childers and Wingo 1968). Some species (e.g., *C. nanus* and *C. elemae*), which emerge later, have seldom been seen as larvae immediately in our early spring samples. These species may only hatch and complete their development after spring temperature conditioning.

The quality of a tree hole may also affect development time and modify the relative emergence sequence of tree hole *Culicoides*. Hair and Turner (1966) and Linley (1969) have shown that larval development of *Culicoides* depends on nutritional needs related to specific micro-organisms. From our study, when a species such as *C. guttipennis*, *C. arboricola*, or *C. villospennis* occurs in a tree hole outside of its optimal habitat, emergence is delayed.

There are various partitioning strategies used by animals. Invertebrates usually separate by temporal relationships (Schoener 1986) while higher animals, such as birds, more commonly

Table 1. Species associations showing the number of times (no./no.) that the emergence relationship detailed in Fig. 2 held when examining individual tree holes for all collections in our study. Underlined numbers show number of times that only a single species occurred in a tree hole. Hyphen shows that the 2 species were not collected from the same tree hole.

Species	Species associations									
	gut	vil	arb	sno	par	lah	hin	nan	foo	ele
<i>C. guttipennis</i>	<u>31</u>	5/6	16/20	2/5	0/2	2/2	0/1	1/3	1/1	1/2
<i>C. villospennis</i>		<u>6</u>	4/5	1/1	—	1/1	—	0/2	1/1	2/2
<i>C. arboricola</i>			<u>4</u>	2/3	2/2	1/1	1/3	3/3	1/1	1/2
<i>C. snowi</i>				<u>0</u>	3/3	2/2	1/1	4/4	4/5	2/2
<i>C. paraensis</i>					<u>3</u>	1/1	—	—	2/2	2/2
<i>C. lahillei</i>						<u>3</u>	2/2	0/1	—	—
<i>C. hinmani</i>							<u>0</u>	2/2	1/1	1/1
<i>C. nanus</i>								<u>0</u>	4/4	2/2
<i>C. footei</i>									<u>0</u>	1/2
<i>C. elemae</i>										<u>0</u>

use partitioning on the basis of habitat (Schoener 1974). In our study of tree hole *Culicoides*, both partitioning models were evident and may depend on the overwintering and nutritional needs of the different species.

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