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Spatial and Seasonal Distribution of Potential Vectors of Hemorrhagic Disease Viruses to Peninsular Bighorn Sheep in the Santa Rosa Mountains of Southern California

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ABSTRACT: Blood-feeding midges (*Culicoides* sp. and *Leptoconops* sp.) were sampled in the Santa Rosa Mountains, Riverside County, California (USA), to determine which species might be involved in the transmission of bluetongue and epizootic hemorrhagic disease viruses to peninsular bighorn sheep (*Ovis canadensis cremnobates*). Host-seeking midges were sampled with CO_2-baited suction traps over a period of 30 mo. Nineteen species of *Culicoides* and seven of *Leptoconops* were collected. Five of the *Culicoides* sp. recovered are previously undescribed. The most abundant and widely distributed *Culicoides* sp. during spring (presumed virus transmission period to lambs) were *C.* (*Selfia*) *brookmani*, *C. variipennis*, *C.* (*Avaritia*) sp. (a new species near *C. pusillus*), and *C. lahontan*. Of these, *C. brookmani* (all elevations) and *C.* (*Avaritia*) sp. (elevations >750 m) were common in the mountainous terrain inhabited by bighorn sheep. *Culicoides variipennis*, a vector of bluetongue virus in agricultural settings, and *C. lahontan* were numerous in sandy washes but were much less common in the mountains themselves. *Leptoconops belkini* and *L. foulki* were occasionally common in upper Deep Canyon in spring (April–June), while *L. torrens* was very abundant in the same area for 2 wk following heavy summer rains. Parity (an indicator of longevity and success in finding hosts and oviposition sites) in mountain areas was very low in *C. variipennis* (5%), low-moderate in *C.* (*Avaritia*) sp. (13%) and *C. lahontan* (21%), and relatively high in *C. brookmani* (40%). Vectorial capacity of *Culicoides* spp. for these hemorrhagic disease viruses is discussed, and it is suggested that species in addition to *C. variipennis* be considered as potential vectors of hemorrhagic disease viruses to desert bighorn sheep.

Key words: Orbivirus, *Culicoides* sp., bluetongue virus, epizootic hemorrhagic disease virus, epizootiology, bighorn sheep, *Ovis canadensis cremnobates*.

INTRODUCTION

Bluetongue (BTV) and epizootic hemorrhagic disease (EHDV) viruses can be severe pathogens of wild ruminants, causing extensive hemorrhaging, edema, and erosion of epithelium in the oral cavity, as well as predisposing infected animals to secondary bacterial or viral pneumonia (Hoff and Trainer, 1981). Based on serological surveys, black-tailed and mule deer (*Odicoileus hemionus*), pronghorn antelope (*Antilocapra americana*), tule elk (*Cervus elaphus nannodes*), peninsular bighorn sheep (*Ovis canadensis cremnobates*), and some populations of Nelson's bighorn sheep (*O. canadensis nelsoni*) consistently are exposed to BTV and/or EHDV in California (Clark et al., 1985; Jessup, 1985).

The status of the relatively rare peninsular bighorn is of particular concern, and one of the largest remaining herds inhabits the Santa Rosa Mountains. In an analysis of nearly 30 yr (1953 to 1982) of population composition data for this range, Wehausen et al. (1987) confirmed a marked decline in summer/fall lamb : ewe ratios beginning in 1977, but the decline possibly began some years before. High lamb mortality due to pneumonia appears to be influenced by one or more pathogens prevalent in the population (DeForge and Scott, 1982). Based on serology, levels of exposure to contagious ecthyma, BTV, EHDV, and parainfluenza-3 (PI-3) are high (>40% seropositivity) (Turner and Payson, 1982; DeForge et al., 1982; Clark et al., 1985; Jessup, 1985). All four common United States serotypes of BTV (10, 11, 13, 17) and one of EHDV have been isolated from bighorn sheep in or near the Santa Rosa Mountains (Clark et al., 1985; Jessup, 1985).

Transmission of BTV and EHDV is pri-

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marily through the blood-feeding activities of biting midges in the genus *Culicoides* (Gibbs and Greiner, 1988). In North America, the only proven vector is *C. variipennis*, though other species are suspect in certain areas (Jones et al., 1981; Gibbs and Greiner, 1988). Given the potential importance of BTV and EHDV in desert bighorn sheep populations in southern California, a study was initiated to determine the *Culicoides* spp. present, their spatial distribution, and their seasonal abundance in the Santa Rosa Mountains.

MATERIALS AND METHODS

Study area

The Santa Rosa Mountains extend from Palm Springs approximately 56 km southeast and range in elevation from 120–2,657 m; they are part of a western extension of the Sonoran desert (MacMahon, 1979; Wehausen et al., 1987). Topography varies from rolling foothills to steep, rocky escarpments and is most diverse on the eastern side of the range. Most of the watershed also is on the eastern side, which includes most of the bighorn sheep range (Wehausen et al., 1987). Rainfall averages 9 to 10 cm/yr but is highly variable; the majority of precipitation occurs between November and March, with the remainder during periodic summer storms from July to September (Ting and Jennings, 1976).

Vegetation on hillsides at lower elevations is dominated by creosote bush (*Larrea tridentata*), brittle-bush (*Encelia farinosa*), burro-bush (*Ambrosia dumosa*), and cactus such as the golden cholla (*Opuntia echinocarpa*), buckhorn cholla (*O. acanthocarpa*), and barrel cactus (*Ferocactus acanthodes*). Agave (*Agave deserti*) and Mohave yucca (*Yucca schidigera*) become more common at elevations above 500 m, giving way to juniper (*Juniperus californica*), manzanita (*Arctostaphylos glauca*), and pinon pine (*Pinus monophylla*) at elevations above 750 to 1,000 m. In the drainages native fan palms (*Washingtonia filifera*), cottonwood (*Populus fremonti*), willows (*Salix exigua*) and other trees can be found.

Insect collecting and handling

Most insects were collected using small, battery-powered Centers for Disease Control (CDC)-type miniature suction traps (Sudia and Chamberlain, 1962) baited with approximately 1 kg dry ice (CO_2) and a small incandescent light bulb. Traps were deployed, usually on vegetation at a height of 0.6–1.0 m, approximately 1 to 2 hr before sunset and were retrieved 1 to 2 hr after sunrise. Insects attracted to the vicinity of the trap were blown into a fine mesh (nylon organdy) catch bag, where they were alive when retrieved the next morning. The insects were returned to the laboratory, immobilized by freezing for 15 to 30 min, and transferred to 70% ethanol for later identification and counting. Additional specimens were collected by aspirator from window lights at the Deep Canyon research station and were placed directly into 70% ethanol. Reference specimens collected from Deep Canyon by E. Schlinger in the 1960's and deposited in the Entomology Collection at the University of California (Riverside, California 92521, USA) were examined and noted in the listing of species known from that location.

In many members of the genus *Culicoides*, a dark, burgundy-red pigment is deposited just beneath the abdominal cuticle following digestion of a blood meal and development of an egg batch (Dyce, 1969). In *C. variipennis*, both abdominal pigment and changes in tergite patterns are useful in determining parity (Potter and Akey, 1978; Akey and Potter, 1979; Mullens and Schmidtmann, 1982). Some species of *Culicoides* are autogenous (i.e., they can develop a batch of eggs without a blood meal) (Linley, 1983), but the regular recovery of nulliparous (unpigmented) females in CO_2-baited traps suggests that a given species probably is anautogenous. Females of species for which this method was appropriate were age-graded externally into nulliparous and parous categories, and parity was confirmed in representative collections by ovarian dissection (Mullens and Schmidtmann, 1982). Parity estimates allowed inferences regarding survivorship and the success of those species in finding hosts and oviposition sites (e.g., Mullens and Rutz, 1984).

No recent keys exist for the *Culicoides* spp. of California, which were identified with the aid of published wing photographs and morphometric data (Wirth et al., 1985), by comparison to reference material from the Entomology Collection at the University of California (Riverside, California 92521, USA) and through correspondence with W. W. Wirth, who kindly agreed to examine representative material. All *Leptoconops* (another blood-feeding genus in the Ceratopogonidae) were identified to genus, but were not necessarily identified to species. Rather, a subsample of each collection was slide-mounted, and these individuals were identified to the species level using keys by Wirth and Atchley (1973) and Clastrier and Wirth (1978).

Sampling sites

Several drainages directly to the south and west of Palm Desert (33°42′N, 116°22′W) were

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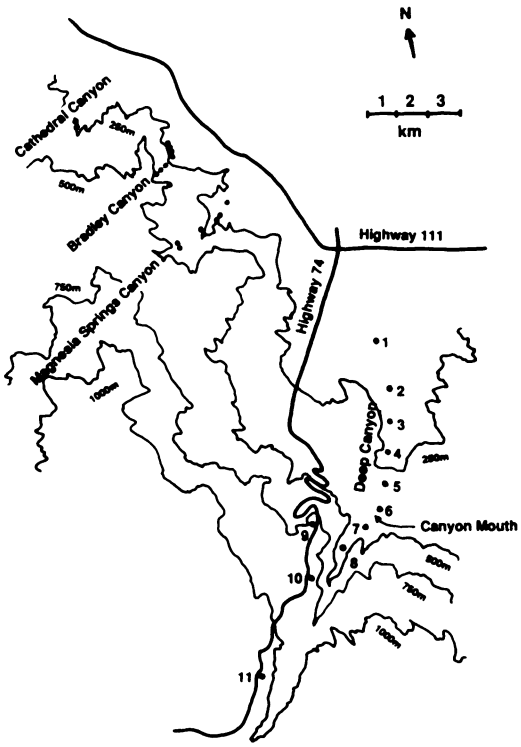


FIGURE 1. Map of Santa Rosa Mountain study area. Black dots indicate sampling locations. Collecting sites in Deep Canyon are designated by numbers (1–11).

sampled from January to June 1988 (Fig. 1). Deep Canyon drains a major area of the north and east slopes of the Santa Rosa Mountains, and the University of California maintains the Philip L. Boyd Deep Canyon Desert Research Center at the canyon mouth. Data on temperature and rainfall were obtained from records gathered since the early 1960's at this location. Sampling was conducted at two week intervals at the research station (Fig. 1, position 6, hereafter called DC6). Two other traps were deployed at 2 wk intervals approximately 2 km into Deep Canyon itself (DC8). During this period trapping also was conducted at irregular intervals in Cathedral Canyon, Bradley Canyon, and several positions along the length of Magnesia Springs Canyon. Samples from Deep Canyon and Magnesia Springs Canyon also were taken irregularly during much wetter spring periods in 1983 and 1984.

From late March to early May 1988 (three sample dates), additional traps were deployed at 1 km intervals down the length of Deep Canyon. These sites ran from 2 km above the research station (well into the canyon itself at DC8) to 3 km below it (open sandy wash at DC3).

From June 1988 to June 1990, efforts were concentrated on the Deep Canyon drainage at six regular sampling positions (Fig. 1). Samples were collected at 2 wk intervals, except when collections at the higher elevations were suspended in January and February due to low temperatures. The first three positions were at lower elevations (130 to 290 m) and included (1) the research station (DC6), (2) approximately 2 km down the wash at the 0.7 km marker (DC4), and (3) the bottom of the wash on a berm behind the Living Desert Reserve (DC1), approximately 6 km below the research station. The other three sampling stations were along Hwy 74 near the Deep Canyon rim at higher elevations (750 to 1,165 m) within peninsular bighorn sheep range. These were (4) Carrizo Canyon turnout near the access gate (DC9), (5) east side of the road across from Bighorn Drive (DC10) and (6) near the parking area for Bighorn Overlook (DC11).

RESULTS

Collections

Nineteen species of *Culicoides* and seven species of *Leptoconops* either were collected in the present study or were known from prior records from Deep Canyon. The *Culicoides* spp. were as follows: *C. brookmani*, *C. cockerellii*, *C. cacticola*, *C. copiosus*, *C. defoliarti*, *C. freeborni*, *C. insolatus*, *C. lahontan*, *C. mohave*, *C. ryckmani*, *C. sitiens*, *C. torridus*, *C. variipennis*, *C.* (*Selfia*) sp., *Culicoides* (*Avaritia*) n. sp. near *pusillus*, *Culicoides* n. sp. *guttipennis* group, *Culicoides* n. sp. near *lahillei*, *Culicoides* n. sp. near *palmerae*, and *Culicoides* n. sp. *piliferus* group. The *Leptoconops* spp. included: *L. americanus*, *L. belkini*, *L. foulki*, *L. knowltoni*, *L. pertussi* group, *L. torrens*, and *L. werneri*. Five of the *Culicoides* spp. (26% of the total species) collected in this study were previously undescribed. A description is in preparation for *Culicoides* (*Avaritia*) n. sp. near *pusillus* (Wirth and Mullens, unpubl. data), which was one of the most abundant of all species collected. Of the remaining undescribed species collected in this study, only *Culicoides* n. sp. near *lahillei* was collected regularly. One hundred eighty six females of this species were collected, with 125 (67%) captured at the higher elevation

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locations in Deep Canyon (DC10 and DC11).

A substantial number of the total *Culicoides* spp. were members of the *C. copiosus* group (*C. cacticola, C. copiosus, C. insolatus, C. ryckmani, C. sitiens*, and *C. torridus*). Relatively few individuals of this group were collected in the CO_2-baited traps, and most were *C. cacticola* or *C. ryckmani*. Of 79 *C. cacticola* in the traps, 74 (94%) were from the canyon floor (DC6 and DC4). Of 220 *C. ryckmani*, 178 (81%) were from the higher elevations on the canyon rim (DC9–DC11). In contrast to their scarcity in the traps, both these species were abundant at window lights at DC6; using a mouth aspirator, dozens of each could be collected within 10 to 20 min on some nights. A few of these specimens appeared to be engorged with blood.

Species composition versus location

Data for three nights' trapping along a 5 km longitudinal transect of Deep Canyon are presented in Figure 2. Well into the canyon itself (DC8), *C. brookmani* was the only species collected in numbers. A few *C. variipennis* were collected there as well. *Culicoides brookmani* was most abundant at the Deep Canyon Station (DC6) and declined in abundance further down the wash. Several dozen male *C. brookmani* were collected at window lights for positive identification. In contrast to *C. brookmani*, the other common species (*C. variipennis, C. lahontan*, and *C. mohave*) all were collected in higher numbers in the wash below Deep Canyon Station (DC3–5).

These data were consistent with long-term data from the regular collecting locations in the bottom of Deep Canyon (DC1, DC4, DC6). *Culicoides variipennis* dominated trap collections (93.8% of the total) in the lower wash at DC1 (Fig. 3A). Further up the wash, *C. brookmani* became more common (Fig. 3B), until it comprised 93.4% of all *Culicoides* spp. collected at the canyon mouth at DC6 (Fig. 3C). Other species found commonly at DC6

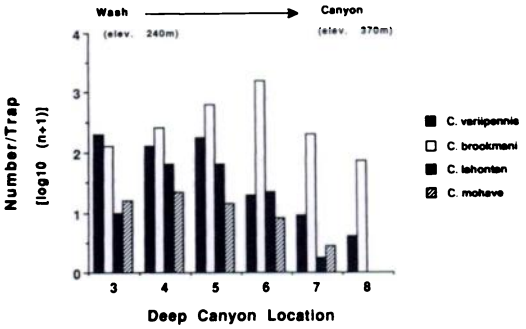


FIGURE 2. Mean number of *Culicoides* spp. collected over three nights at each of 6 positions (see Fig. 1) along a longitudinal transect of the Deep Canyon drainage in spring 1988. Collecting sites 1 km apart.

included *C. variipennis* (3.1%), *C. lahontan* (1.2%), *C. mohave* (1.2%) and *C. (Avaritia)* n. sp. near *pusillus* (0.5%) (Fig. 3C). Activity of *Leptoconops* spp. also was higher near the canyon mouth, with a total of 3,707 at DC6, 1,228 at DC4, and only 28 at DC1.

At the higher elevations, *C. brookmani* still was most common, while *C. variipennis* was collected regularly but in low numbers (Fig. 3D–F). Numbers of *C. lahontan* equalled or exceeded those of *C. variipennis*. At higher elevations *C. (Avaritia)* n. sp. near *pusillus* became increasingly common, until it comprised 30% of the total at DC11 (Fig. 3D–F). *Leptoconops* spp. were seldom captured at the upper elevations, with a total of 68 specimens from DC9, 140 from DC10, and 28 from DC11 over the 2 yr duration of the study in those locations.

Seasonal abundance

High temperatures in the winter seldom were below 15 C, and a hard freeze did not occur during the study period (Fig. 4). Maximum temperatures between July and Spetember often averaged over 40 C. Late fall and early winter rains were slightly above average for 1987 (89 mm for October and December), whereas the same periods in 1988 and 1989 were notable for their very low precipitation. Substantial

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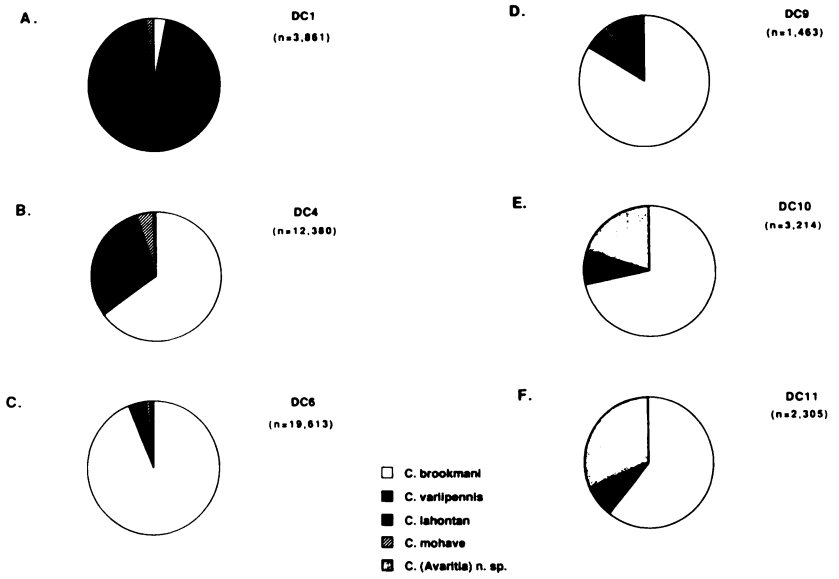


FIGURE 3. Total number of *Culicoides* spp. and proportions of the principal species collected at the primary Deep Canyon sampling sites from January 1988 to June 1990 (DC6) or June 1988 to June 1990 (DC1, DC4, DC9–11).

summer rains occurred in mid-August 1988 and in July 1989 (Fig. 4).

The most abundant species, *C. brookmani* and *C. variipennis*, could be collected during any month of the year. However, both species exhibited spring and fall activity peaks (Fig. 5A–D). A large emergence of *C. variipennis* occurred in the lower wash (DC1) 3 to 6 wk after heavy August 1988 rains (Fig. 5A). Temporary pools were created approximately 50 to 100 m from the trapping site, where larvae of *C. variipennis* were dense approximately 2 wk after the rains. At the Deep Canyon Station (DC6), *C. variipennis* was most common in the spring (March and April), but numbers generally declined over the 30 mo trapping period (Fig. 5B). *Culicoides brookmani* also was most abundant in the spring (March to June), with a second period of activity in September and October (Fig. 5C). There appeared to be somewhat fewer *C. brookmani* in 1989 and 1990 versus 1988, though this trend was less notable than for *C. variipennis*. A spring activity peak also was observed for *C. lahontan*, which was markedly more abundant in 1988 (Fig. 5E). The new species of *Avaritia* was sporadically abundant, with some indication of spring and fall peaks (April to June and October) at the higher elevations (Fig. 5F, G). *Culicoides mohave* was most abundant in the summer at the lower elevations.

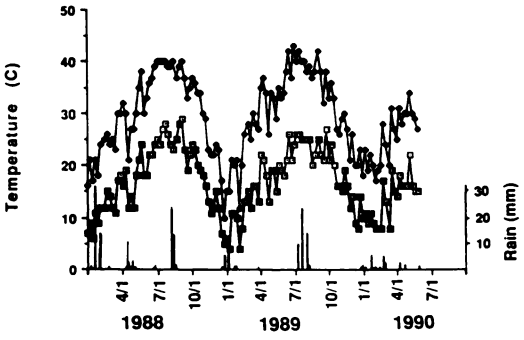


FIGURE 4. Average weekly maximum and minimum air temperatures and rainfall (bars) data at the Philip L. Boyd Deep Canyon Desert Research Center at the Deep Canyon mouth (DC6).

Seasonal abundance of *Leptoconops* spp. is presented in Figure 6. Based on identification of randomly selected, slide-mounted individual females, the spring

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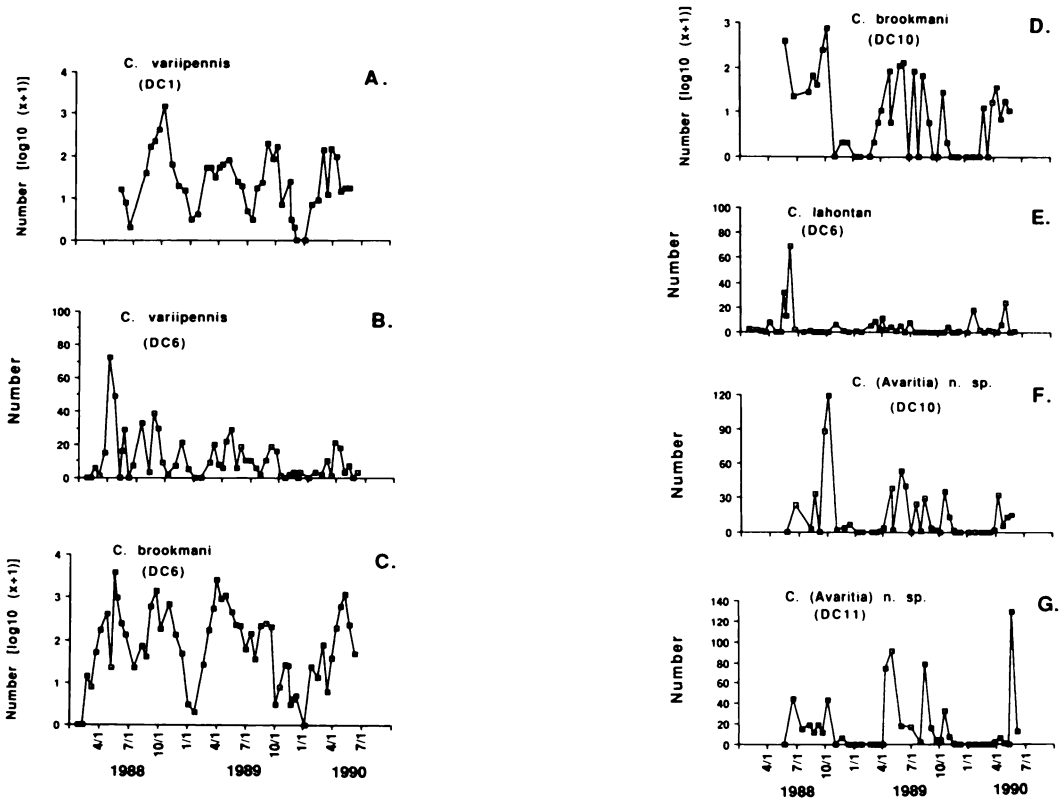


FIGURE 5. Seasonal abundance of selected *Culicoides* spp. in Deep Canyon. A). *C. variipennis* in the lower wash (DC1), B). *C. variipennis* at the canyon mouth (DC6), C). *C. brookmani* at the canyon mouth (DC6), D). *C. brookmani* on the canyon rim (DC10), E). *C. lahontan* at the canyon mouth (DC6), F). *C.* (*Avaritia*) n. sp. on the canyon rim (DC10), G). *C.* (*Avaritia*) n. sp. on the canyon rim (DC11).

collections (April to June) were mainly members of the *L. kerteszi* group, particularly *L. belkini* and *L. foulki*. Numbers generally were low, but these species were common (sometimes >100/trap/night) in a few late March and early April collections each year. Slide-mounted specimens from DC6 indicated a ratio of *L. belkini*: *L. foulki* of 2.4:1. We also collected occasional specimens of *L. americanus* and *L. knowltoni*. Substantial, synchronous emergences of *L. torrens* occurred after summer rains in 1988 and 1989, but numbers declined rapidly 2 to 3 wk after the rains (Fig. 6). During these periods biting intensity on humans was very high.

Parity profiles

Parity data are presented for the major species, by Deep Canyon location, in Table 1. Overall parity was fairly high (36 to 45%) in *C. brookmani*. There were few significant differences (pairwise chi-square comparisons, $P > 0.05$) according to trapping location, though parity at the DC4 location was significantly higher due to the large sample size. Parity was low-moderate (12 to 25%) in *C. lahontan*, and was highest at the canyon mouth (DC6). *Culicoides* (*Avaritia*) n. sp. exhibited a low-moderate level of parity (12 to 14%) at the higher elevations, with no significant difference between DC10 and DC11. Average parity in *C. variipennis* decreased significantly ($P < 0.05$) from a low-moderate level of 11.5% in the lower wash (DC1) to a very low 4.7% at the canyon mouth (DC6).

Seasonal periods of higher parity in *C. variipennis* (Fig. 7A, B) and *C.* (*Avaritia*)

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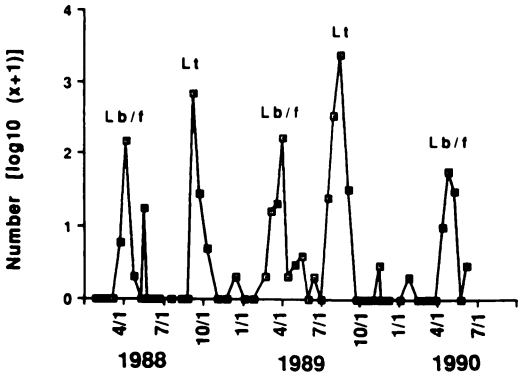


FIGURE 6. Seasonal abundance of *Leptoconops* spp. at the mouth of Deep Canyon (DC6). Dominant spp. in the collections based on species determinations on subsamples of total collections are shown by: Lb/f, *L. belkini* and *L. foulki*, Lt, *L. torrens*.

n. sp. (Fig. 7D) lagged slightly behind peak activity periods. This was particularly evident in *C. variipennis*, with small but distinct increases in parity in spring and especially fall. Parity in *C. brookmani* did not follow a distinct pattern relative to major activity periods (Fig. 7C).

Collections from other Santa Rosa mountain locations

Magnesia Springs Canyon was sampled between March and June on 4 dates in 1983 and 1984 (8 trap nights) and 4 dates in 1988 (16 trap nights). The predominant species were *C. brookmani* and *C. variipennis*. Direct comparisons were made between traps deployed in the same ridge location, approximately 1 km into the canyon (four trap nights/period). A total of 474 *C. brookmani* was collected in 1983 and 1984, versus only 28 in 1988. For *C. variipennis*, the total was 8 in 1983 and 1984 and four in 1988. Also collected in Magnesia Springs Canyon were *C. lahontan* and *C. mohave*. Bradley Canyon was sampled on 10 and 24 May 1988 (10 trap nights). *Culicoides variipennis* (44 total) and *C. brookmani* (38 total) again were the dominant species, but *C. mohave* also was collected. A single trapping date on 23 February 1988 (two traps) in Cathedral Canyon yielded one *C. variipennis*.

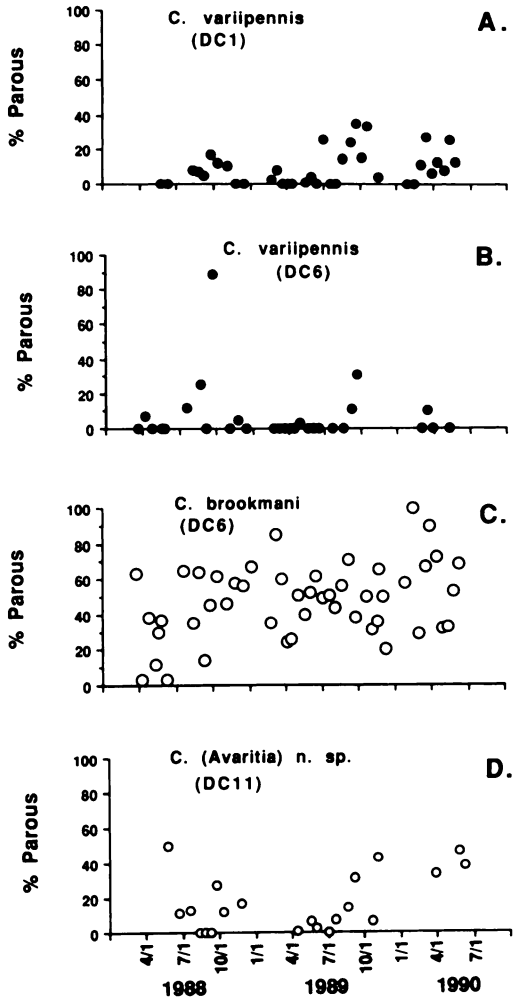


FIGURE 7. Seasonal parity levels in selected *Culicoides* spp. Only data points representing ≥5 females shown. A). *C. variipennis* in the lower Deep Canyon wash (DC1), B). *C. variipennis* at the Deep Canyon mouth (DC6), B., C). *C. brookmani* at the Deep Canyon mouth (DC6), D). *C. (Avaritia)* n. sp. on the Deep Canyon rim (DC11).

DISCUSSION

The rich assemblage of *Culicoides* spp. at first seems surprising in such a desert setting, since most require aquatic or semi-aquatic habitats as immatures. On a microhabitat scale, however, habitat diversity in the Santa Rosa Mountains is high, including permanent streams, seasonal rock pools, damp sand and organic material in rock crevices and roots of riparian vege-

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TABLE 1. Average parity in females of common *Culicoides* spp. versus trap location (see Fig. 1) in Deep Canyon, Santa Rosa Mountains, California (USA).

Species	Deep Canyon location					
	DC6	DC4	DC1	DC9	DC10	DC11
C. brookmani						
number	13,862	7,309	—	1,169	2,088	1,302
parity (%)	37.9%b*	44.8%a	—	40.1%b	36.3%b	38.2%b
C. (Avaritia) n. sp.						
number	—	—	—	—	543	979
parity	—	—	—	—	13.8%a	12.4%a
C. lahontan						
number	192	252	—	—	—	90
parity	25.0%a	17.9%ab	—	—	—	13.3%b
C. variipennis						
number	805	2,450	3,627	—	95	—
parity	4.7%	9.8%b	11.5%a	—	6.3%abc	—

* Row values followed by the same letter are not significantly different ($P > 0.05$) by chi-square comparisons on the numbers parous/nulliparous.

tation, algal mats, rotting cacti, etc. Because these *Culicoides* spp. rarely bite humans in this area, their presence in high numbers would not be appreciated or recognized by a casual observer. Likewise, the large numbers of *Culicoides* spp. in CO_2-baited traps quite distant from any apparent developmental sites suggest the attractiveness of such traps (or probably vertebrate hosts) in such a dry, host-poor habitat may be quite high, as may be the dispersal abilities of the species involved. Wirth et al. (1985) noted 144 North American species of *Culicoides*, approximately 60 of which had distributions which include, or likely could include, California. The fact that five of 19 species collected in a limited study in a single desert mountain range currently are undescribed underscores the lack of even the most basic information on many species in the genus.

The concept of vectorial capacity was developed for malaria (MacDonald, 1952), but is equally relevant for arboviruses such as BTV and EHDV. The basic components of vectorial capacity are biting intensity, vector competence (susceptibility of the insect host to virus replication), and vector longevity. The parameters of vectorial capacity operate in the context of existing environmental conditions which allow variable levels of vector-host contact. A number of the species collected during this study in traps baited with CO_2 were relatively uncommon. If one assumes this would correlate with lower biting intensity on bighorn sheep, the likelihood of their involvement in BTV or EHDV transmission is reduced.

The *C. copiosus* group, for example, comprised 32% (six of 19) of the total number of *Culicoides* spp. collected. This group utilizes decomposing cactus as a developmental site (Ryckman, 1960). Based on the collection of at least *C. ryckmani* and *C. cacticola* in large nubmers at light in Deep Canyon, they were common in the area, but they were uncommon in the traps. This suggests that they either are not blood feeders or are not attracted to CO_2. Some apparently engorged specimens were collected at light. Ryckman (1960) collected engorged *C. ryckmani* from a finch nest. Ongoing host preference studies in Deep Canyon suggest that both *C. cacticola* and *C. ryckmani* feed on birds, but generally not on mammals (B. A. Mullens and C. E. Dada, unpubl.), and cues other than CO_2

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may be more important for host orientation in this group.

Of the remaining *Culicoides* spp. which were collected more routinely, *C. mohave* was common in the wash, but was much less common in the higher elevation areas where bighorn sheep were found. The species nevertheless was widespread in the Santa Rosa Mountains. It also was not common in the presumed spring period of BTV and EHDV transmission, being collected in larger numbers in summer. *Culicoides mohave* was abundant in the lower Coachella Valley near the Salton Sea in August (Brenner et al., 1984b), and Foulk (1966) found immatures of this species in a saline drainage in the same area. The host-seeking females collected in the Santa Rosa Mountains conceivably could have dispersed from similar habitats in the lower canyon wash areas at the edges of the Coachella Valley. Brenner et al. (1984b) collected a marked female *C. mohave* 6 km from the release site after only 30 hr, though most were recaptured within 2.5 km.

The status of *Leptoconops* spp. as potential BTV or EHDV vectors is unknown. In contrast to most *Culicoides*, *Leptoconops* spp. tend to seek hosts during the day, so our trapping probably underestimated their abundance. Both Foulk (1969) and Brenner et al. (1984a) showed a bimodal attack pattern (just after sunrise and just before sunset) by host-seeking midges in the *L. kerteszi* complex. Our pattern of trap placement and retrieval usually would have included the dusk and dawn activity periods, but the midday attack period was missed. Many *Leptoconops* spp. are well known for their propensity to bite mammals (Wirth and Atchley, 1973), and are obvious to humans in the Santa Rosa Mountains due to their human-biting habit. The extreme periodicity of *L. torrens* and timing of its occurrence after summer rains, as well as very low parity rates, have been noted by Brenner and Wargo (1984). These factors would argue against serious consideration of *L. torrens* as a BTV/EHDV vector in this system. *L. belkini* and *L. foulki* were present over a longer time during the spring, but their numbers tended to be relatively low. They were common in a few spring collections, however, and Brenner et al. (1984a) documented high parous rates (30 to 60%) for *L. foulki* and *L. knowltoni* near the Salton Sea.

Based on seasonal (spring) abundance, spatial distribution, and parity profiles, four *Culicoides* species would be most suspect in BTV and/or EHDV transmission to peninsular bighorn sheep. These are *C. lahontan*, *C.* (*Avaritia*) n. sp., *C. variipennis*, and *C. brookmani*. They are discussed individually below.

Culicoides lahontan is part of the *C. cockerellii* group, which includes *C. cockerellii*, *C. freeborni*, and *C. saltonensis* (from prior collections in the Coachella Valley). Of these, *C. freeborni* was collected regularly, but in lower numbers than *C. lahontan*. Peak activity of *C. lahontan* occurred in the late spring (May and June). Our data suggest that abundance of this species depends on winter/spring rainfall patterns, which may impact availability of immature developmental habitats. Though collections were somewhat sporadic, *C. lahontan* was taken in large numbers (up to 140/trap night) in late spring of 1983 and 1984 in Deep Canyon and Magnesia Springs Canyon. Both years had substantial rainfall. We found *C. lahontan* to be common in Deep Canyon only in 1988, after a winter-spring period of approximately average rain; it was relatively rare in 1989 and 1990, both very dry years. It was quite widely distributed in the Santa Rosa Mountains at both low and high elevations within sheep range, but was captured in highest numbers in the upper Deep Canyon wash. Parity in *C. lahontan* appeared to be moderate (13 to 25%) and higher at the lower elevations. This suggests *C. lahontan* was successfully locating hosts and oviposition sites and survived to seek a second (or subsequent) blood meal in these habitats. Little is known of the biology of *C. lahontan*, particularly with

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regard to its host-feeding patterns or vector competence for BTV or EHDV. Kramer et al. (1990) isolated BTV from a pool of *C. cockerellii* group midges in Colorado. Wirth and Blanton (1969) noted several mammal-feeding records, including deer and rabbits for *C. freeborni*.

C. (*Avaritia*) n. sp. was increasingly abundant in the higher elevations of Deep Canyon in the spring; a number of bighorn ewes with lambs were observed in the spring in the area near collecting sites DC9 and DC10, where *C.* (*Avaritia*) n. sp. comprised 9 to 19% of the total *Culicoides* spp. It was rarely collected in moderate numbers (20 to 30/trap night) at the mouth of Deep Canyon (DC6), but was absent further down the wash. Its very small size (wing length 0.6 mm) would allow it to escape from all but the finest netting (the organdy used in the present study was smaller than 100 mesh), and this may explain why it has not been noticed earlier. As with many of the described species, almost nothing is known of its biology. Parity is low-moderate (12 to 14%), suggesting *C.* (*Avaritia*) n. sp. is locating hosts and oviposition sites. This species is of particular interest due to the fact that the established BTV vectors in the old world, particularly the Afrotropical region and Australia, are in the subgenus *Avaritia* (Wirth and Dyce, 1985; Meiswinkle, 1989).

Culicoides variipennis currently is the only proven vector of BTV and EHDV in North America (Gibbs and Greiner, 1988). It should be emphasized that nearly all studies, however, have been done in agricultural areas, where the biology of *C. variipennis* is relatively well known. Immatures develop at high densities in surface mud (or sometimes algal mats) near the edges of either manure-polluted or saline habitats, but they may be found in a wide variety of aquatic habitats (Mullens, 1989). The species readily feeds on mammals (Zimmermann and Turner, 1983a). Many populations of *C. variipennis* are susceptible to BTV replication, though substantial differences exist among and within populations (Jones and Foster, 1978). In one instance, *C. variipennis* was found to be involved in EHDV transmission to whitetailed deer in Kentucky (Foster et al., 1977).

In temperate areas where *C. variipennis* activity has been documented, the primary activity period occurs in the summer and fall (Barnard and Jones, 1980; Mullens and Rutz, 1983). In dairy wastewater ponds in southern California, the peak abundance of *C. variipennis* occurs in the fall (Mullens and Lii, 1987), a period which coincides with increased BTV seropositivity and isolations from domestic ruminants (Osburn et al., 1981). In Florida, however, *C. variipennis* exhibited a spring-summer pattern (Kramer et al., 1985). In the present study, adults of *C. variipennis* were present year-round, with distinct spring and fall peaks. These probably reflect seasonal availability of surface water. There was a general tendency for *C. variipennis* catches to decline over the study period, which also could have been influenced by low winter–spring rainfall in 1988–89 and 1989–90. The large peak in adult emergence in September and early October 1988 in the lower wash (DC1) was probably the result of August rains, which created a large, temporary developmental site nearby. Interestingly, this substantial emergence was not particularly evident 6 km up the wash at DC6.

The combination of spatial distribution and parity is most revealing with regard to vectorial capacity of *C. variipennis*. While this species was widely distributed in the Santa Rosa Mountains generally and Deep Canyon specifically, by far the greatest numbers of *C. variipennis* were found at lower elevations in the wash. It was consistently much less common in areas frequented by bighorn sheep. More significantly, the parity in *C. variipennis* was dramatically less than in agricultural settings, where average parity ranges from 30% to over 45% in this species (Nelson and Scrivani, 1972; Zimmermann and Turner, 1983a, b; Mullens and Rutz, 1984;

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Mullens, 1985; Linhares and Anderson, 1989). A spatial trend in parity also was apparent, with the highest level (11.5%) in the lower Deep Canyon wash (DC1), declining to <5% at the canyon mouth (DC6). Substantially lower numbers of *C. variipennis* at higher elevations also had low parity (6.3% at DC11). There is some evidence for a nulliparous dispersal phase in *C. variipennis* (Zimmermann and Turner, 1983b; Mullens, 1985), and it is possible we were sampling primarily dispersing nulliparous females, which were far from their developmental sites down the wash or in the valley itself. Aquatic sites polluted by manure, or even saline habitats, are rare in the Santa Rosa Mountain study area, and vertebrate host density also is low compared with most agricultural settings. The very low parity suggests that *C. variipennis* is not very successful in locating hosts and/or oviposition sites, and its survivorship in such a severe environment also could be low. The above factors would tend to reduce vectorial capacity for pathogens such as BTV or EHDV.

Culicoides brookmani is a member of the subgenus *Selfia*, a group with clear wings and unsclerotized spermathecae. Because these features are instrumental in identification, females generally cannot be identified with certainty. A few larger females were collected, and are tentatively being categorized as another (unknown, pending collection of males) species in the subgenus *Selfia*. However there is no question that the vast majority of specimens were *C. brookmani*, judging from the fact that all males examined were unmistakably this species.

This species was by far the most abundant *Culicoides* sp. in bighorn sheep habitat in the Santa Rosa Mountains. Numbers at the mouth of the canyon (DC6) sometimes exceeded 3,000/trap/night. Their peak spring activity period began in April and continued through June, though, like *C. variipennis*, they were present basically year-round. The paucity of specimens collected in the lower wash suggests *C. brookmani* was relatively restricted to the mountain areas and nearby washes. The parity rate also was high, averaging approximately 40%. Unlike *C. variipennis*, parity was quite similar regardless of trapping location, perhaps indicating dispersal polymorphism is not marked in *C. brookmani*. High parity indicates *C. brookmani* was surviving to the parous stage and was successfully locating hosts and oviposition sites. While numbers of *C. brookmani* fluctuated seasonally, parity trends did not follow in any clear pattern, which may reflect a prolonged period of emergence and/or a lack of distinct cohorts in nature. Alternatively, our sampling interval may not have been frequent enough to detect emergences clearly.

Little is known of the biology of *C. brookmani*. Atchley (1970) reared this species on two occasions from a small, algae-laden stream and from isolated pools in an intermittent stream, both in desert canyons in Arizona. This type of habitat is common in Santa Rosa Mountain drainages. J. R. Anderson (*in* Atchley, 1970) has collected *C. brookmani* females from deer and one from the ears of a jackrabbit (*Lepus californicus*), so it likely could feed on bighorn sheep as well. Kramer et al. (1990) reported numerous recoveries of rabbit arboviruses (Buttonwillow, Lokern, Main Drain) from *C.* (*Selfia*) spp. While this is not evidence for their involvement in BTV or EHDV transmission, it does suggest that these midges possess some of the other requisite characteristics (e.g., longevity) that influence vectorial capacity, at least in Colorado.

This study emphasizes the potential dangers of extrapolating insect sampling information from one location to another. The *Culicoides* spp. fauna was substantially different in the wash areas at the base of the mountains compared to sites only a few km away in the mountains themselves, and elevation and seasonal differences also were evident. Use of multiple sampling areas over seasonal seasons is advisable to gather reliable information on *Culicoides*

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spp. abundance and distribution, with emphasis on areas frequented by the vertebrate in question (in this case, bighorn sheep). The taxonomic diversity, and the substantial number of new species encountered in this limited study, also underline the need for care in identifications.

The bimodal rainfall pattern in the Santa Rosa Mountains probably influenced the abundance of at least some of the potential vector species of *Culicoides*. Of the primary suspects, *C. lahontan* and *C. variipennis* seemed to be more dependent on seasonal rains than did *C.* (*Avaritia*) n. sp. and *C. brookmani*. This may vary among drainages, however. Deep Canyon, which drains a larger area, had substantially more water in the spring of 1988 (average rainfall year following a sub-normal year) than did Magnesia Springs Canyon. Collections of *C. brookmani* in Magnesia Springs Canyon in 1988 were far less than in the wetter spring periods in 1983 and 1984. Both DeForge and Scott (1982) and Wehausen et al. (1987) have mentioned the possible role of surface water in increasing vector numbers and thereby arbovirus transmission. If abundance is a critical factor in vectorial capacity, and if BTV and/or EHDV are instrumental in lamb mortality, one might expect to see bighorn recruitment rates drop in times of higher rainfall.

Wehausen et al. (1987) pointed out that the two periods of depressed recruitment in the Santa Rosa bighorn population (mid-late 1950's and particularly 1977 to 1982) generally were years of high rainfall. A significant negative relationship between recruitment and April precipitation over the period 1962 to 1976 has also been noted, but certainly could be a statistical artifact (Wehausen et al., 1987). We know little about the generation intervals of most species; *C. variipennis* probably could respond quickly enough to increased availability of surface water in April to become abundant in May. That was the case with temporary pools resulting from heavy August rains in 1988, as *C. variipennis* numbers peaked 3 to 6 weeks later.

Whether or not BTV and EHDV are instrumental in low recruitment in this population of bighorn sheep, it is certain that these viruses are being transmitted. Reducing insect-borne diseases indirectly through vector suppression (e.g., management of developmental sites) is an attractive possibility. Further studies are required to implicate a responsible vector(s) in the Santa Rosa Mountains, including intensified virus isolation attempts with field-collected material, documentation of host-feeding patterns, vector competence studies, and eventual transmission studies. Based on the present studies, we feel that attention should be focused on *C. lahontan*, *C. variipennis*, *C.* (*Avaritia*) n. sp., and particularly *C. brookmani* as potential vectors of BTV and EHDV to bighorn sheep in this range.

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