Population Ecology

Distribution of Caenocholax fenyesi (Strepsiptera: Myrmecolacidae) and the Habitats Most Likely To Contain Its Stylopized Host, Solenopsis invicta (Hymenoptera: Formicidae)

JERRY L. COOK, J. SPENCER JOHNSTON, ROGER E. GOLD, AND S. BRADLEY VINSON

Department of Entomology, Texas A&M University, College Station, TX 77843-2475

ABSTRACT Caenocholax fenyesi Pierce has been collected sporadically throughout the Neotropics and southeastern United States. We present the known distribution of C. fenyesi, including the addition of 5 new distributional records. The distribution of C. fenyesi was evaluated in Brazos County, Texas, as an example of a concise geographic region saturated with Solenopsis invicta Buren, the known host of males. Stylopized S. invicta were collected at only 10 of 25 sites. The distribution of C. fenyesi in Brazos County appeared limited by some factor other than its male host. Stylopized S. invicta were found in all surveyed habitats, although they were more commonly found in savanna and woodland habitats compared with grasslands.

KEY WORDS Caenocholax fenyesi, distribution, behavior

The distribution of most strepsipteran species is poorly known. The myrmecolacid (Strepsiptera: Myrmecolacidae) Caenocholax fenyesi Pierce is known from numerous locality reports, where adult males were collected in traps. The only exception to this was the discovery that a host of male C. fenyesi in Texas is Solenopsis invicta Buren (Kathirithambay and Johnston 1992).

Caenocholax fenyesi is known from 7 southern states in the United States. The first report of C. fenyesi in the United States was from Florida (Frost 1962, 1963), collected in a study at Archbold Biological Station, Highlands County. Meadows (1967) collected C. fenyesi in light traps from 13 additional counties in Florida. One additional Florida county record was added during a study conducted from 1986 to 1992 (Kathirithambay and Peck 1994). Khalaf (1965) collected C. fenyesi in Louisiana from light traps in the vicinity of New Orleans and other areas of southern Louisiana and later from central Louisiana and 2 locations in Hancock County, Mississippi (Khalaf 1969). Johnson and Morrison (1979) reported C. fenyesi from Georgia and Arizona. A single males was collected in 1960 from Madera Canyon in the Santa Rita Mountains, AZ, in the University of Arizona collection is actually the earliest known collection of C. fenyesi in the United States, but the specimen was not identified and reported until several of the above reports were made. Jones et al. (1980) collected C. fenyesi in Baldwin County, Alabama, at light traps, Kathirithambay and Johnston (1992) reported male C. fenyesi with its host, S. invicta, from Brazos County, Texas.

Although most reports are currently from the United States, C. fenyesi appears to have a widespread Neotropical distribution including Cordoba, Mexico (Pierce 1969); Tabasco, Mexico (Kifune 1979); Peten, Guatemala (Kifune 1979); Matagalpa, Nicaragua (Maas and Kathirithambay 1993); Costa Rica (Kathirithambay 1992); Panama (Bohart 1941); Ecuador and Chile (Kathirithambay 1992); Misiones, Argentina (Bohart 1941); Andros Island, Bahamas (Kathirithambay and Peck 1994); and Cuba (Cenaro and Peck 1995).

These collections begin to establish a large geographic range for C. fenyesi. Available collection data establishes a distribution that appears disjunct, but may be a result of sporadic collections. An examination of the distribution of a strepsipteran species within a concise geographic region has never been attempted. A study of this type can lead to better understanding of the distributional pattern and possible separation of populations within the species.

The objective of this study was to provide a better understanding and prediction of the range of C. fenyesi using information obtained throughout this study, along with additional collection records. This information could be useful in determining the potential of using C. fenyesi as a biological control agent of S. invicta. We determine if stylopized S. invicta have a continuous or disjunct distribution within an area where hosts are not a limiting factor, and also determined the prevalence of stylopized S. invicta in this area.

Materials and Methods

Distribution. We examined the distribution of stylopized S. invicta colonies within Brazos County, Texas, from February 1994 to October 1995. We
stylized tend to climb to a high perch and remain in a posture resembling greater flagging before emergence of the strepsipteral (unpublished data). Colonies were provided with water, mealworms, and 5% honey water daily.

Ants suspected of being stylized with male strepsipteral were isolated in petri dishes (35 by 10 mm) for strepsipteral emergence. Any emergence from the colony or from isolated ants was recorded. If no emergence occurred from isolated ants within 48 h, they were dissected or cleared using 10% KOH to check for the triungulin or its exuvium, which is not eliminated by the ant host. The presence of a triungulin or its exuvium in a cleared ant was used to indicate stylization.

The sample of ants previously placed in EtOH was partially cleared in 10% KOH for 7 d at 22°C to check for parasitization. A record was kept of all stylized ants, and results of the grid-site analysis were plotted on a Brazos County map. Sites that contained colonies with stylized ants were evaluated for significant differences in stylization percentages using a 1-way ANOVA (evaluated at α = 0.05) using Minitab Release 10 (Minitab, Inc.).

Habitat. To discover the habitats most likely to contain colonies with stylized ants, we chose an area at the edge of Raintree Subdivision, at the southeast edge of College Station, TX. This area contains 3 distinctive habitat types, each covering ≈300 m in a straight line from one side to the other. The 1st habitat type was post oak-savanna and consisted of grassy areas along with stands of trees, primarily post oak, Quercus stellata Wang. The 2nd habitat type was dense woodland with little to no grass. A trail was the only disturbed area in the woodland habitat region. The 3rd habitat type was grassland, consisting of open pasture with no trees or brush. Two equally spaced sampling sites were established in each of the habitats. We collected 1 colony at each transect site and replicated the experiment 3 times, using other colonies from the same area, over the course of several months. Collections were made in July 1994, March 1995, and July 1995. Colonies were handled as previously described. Results were analyzed using a chi-square test (Minitab Release 10 (evaluated at α = 0.05) to determine if the habitats contained significantly different percentages of stylized ant colonies.

To test further for significant differences between the 3 habitats listed above, additional site collection information for part of a larger study (Cook 1996) was used to produce a larger data set. Each of the 244 collection's habitat type and level of stylization was recorded. The percentage of stylized colonies was compared using a chi-square test to determine if there were significant differences between the habitats. A 1-way analysis of variance (ANOVA) was used to determine if there were significant differences in the percentage of stylized ants within colonies from the different habitats.

Representative voucher specimens were deposited in the Texas A&M University Insect Collection.
Results

Geographic Distribution of *C. fenyesi*. The current known distribution of *C. fenyesi* in the United States is shown in Fig. 2. The current known world distribution is shown in Fig. 3. We collected *C. fenyesi* from 3 additional Texas counties and report on 1 other Texas county where *C. fenyesi* was collected and reported to us. Additionally, we add a new record from Mexico.

We collected *C. fenyesi* from stenopidized ants with a colony brought back to the laboratory from Cook’s Point (Robertson County), TX, on 10 October 1993. Will Godwin collected a male *C. fenyesi* at lights from Democratic Crossing (Madison County), TX, on 3 September 1995. We identified this specimen which is now deposited in TAMUIC. A 3rd Texas county now included in the distribution of *C. fenyesi* is Travis County, from specimens found by Ed Vargo in dissections. Ed Riley, Mike Quinn, and H. Blackman collected a male *C. fenyesi* at UV light on 16 October 1993 from Cameron County, Texas. This specimen is now in TAMUIC. James Woolley collected a single male strepsipteran in a Malaise trap (27–30 July 1993) at Gomez Farias, Tamaulipas, Mexico. The specimen was found in the TAMUIC where we later identified it as *C. fenyesi*. The reported host ant of *C. fenyesi*, *S. incisata*, is not found in this area. However, a closely related fire ant, *Solenopsis geminata* (F.), is common.

Distribution of *Caenochelus fenyesi* in Brazos County, Texas. Ten of the 25 Brazos County sites contained stenopidized *S. incisata*. However, not all colonies from these 10 transect sites contained stenopidized ants.

Twenty-eight of the 60 colonies collected from the 10 sites contained ants stenopidized by *C. fenyesi*. There was no site from which all 5 of the sampled colonies contained stenopidized ants. Frequency of stenopidized colonies, of 6 colonies collected at each site, are as follows: 5 stenopidized colonies at 1 site; 4 stenopidized colonies at 2 sites; 3 stenopidized colonies at 3 sites; 2 stenopidized colonies at 3 sites; 1 stenopidized colony at 1 site; and no stenopidized ants at 15 sites. The mean stenopidization rate of all colonies was 0.4 percent (range, 0–2.5%). The mean stenopidization rate of infected colonies was 0.9 percent (range, 0.5–2.5%). There was no significant difference be-
Table 1. Comparison of pooled data for all colonies collected in Brazos County, Texas, 1993–1996

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>No. colonies</th>
<th>% Infected when stylized</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Stylized</td>
<td>Not stylized</td>
</tr>
<tr>
<td>Dense woodland</td>
<td>35</td>
<td>48</td>
</tr>
<tr>
<td>Post oak-savanna</td>
<td>31</td>
<td>37</td>
</tr>
<tr>
<td>Grassland</td>
<td>9</td>
<td>64</td>
</tr>
</tbody>
</table>

between percentages of stylization in the sites that contained *C. fenyesi* ($F = 0.39; df = 8, 45; P = 0.919$).

The distribution pattern of stylized transect sites appears to be in a zone across the center of the county, except for 1 site at the county's southern edge (Fig. 1). No common factor is known among these sites containing stylized ants.

**Habitat of Stylized *S. incerta*.** Five of 7 colonies collected in the woodland habitat contained stylized ants. One woodland habitat site was collected on only the 1st of the 3 collection dates. On other dates, this site did not have detectable fire ant colonies for collecting. Four of 6 savanna habitat sites and 2 of 6 grassland habitats sites (sites 2 and 3) contained colonies with stylized ants. Thus, stylized ants were in all habitat types, but were more common in woodland and savanna habitats.

The mean percentage of stylized ants in affected colonies was 1.2% for woodlands, 1.0% for savanna, and 0.5% for grasslands. Ants in the grassland habitat had the lowest level of stylization (0.5%), which was found in each of 2 colonies that contained stylized ants. Stylization levels in the savanna and woodland habitats ranged from 0.5 to 3.3% and 0.5 to 2.0% of stylized colonies, respectively. The percentage of stylized ants found in colonies were not significantly different between habitats in this experiment ($F = 1.61; df = 2, 16; P = 0.231$). There was also no significant difference between collection dates ($F = 1.41; P = 0.274$).

Additional habitat information from another study (Cook 1996) is given in Table 1. These collection sites also were from Brazos County but were not randomly chosen as in the previous study. However, the records of all stylized colonies provide a larger number of colonies for comparison of habitats and percentages of stylized ants present. It was not possible to obtain this number of colonies from the habitat experiment site alone. Pooled information, from all sources, is shown in Table 1. Fewer colonies collected from the grassland habitat are stylized, 12.3% (9 of 73), than those found in woodland and savanna habitats, 42.2% (35 of 83) and 35.2% (31 of 88), respectively. These results indicate that the number of stylized colonies in grassland habitats is significantly different from the other habitats ($\chi^2 = 17.548$, df = 2, $P = 0.006$). The stylization level of each stylized colony was 1.2% in woodland habitats, 1.1% in savanna, and 0.8% in grasslands.

**Discussion**

The distribution of *C. fenyesi* appears to be Neotropical, with the southern United States forming its northern limit. More reports have been made from the southern United States than from Neotropical areas, but this phenomenon is likely a result of more intensive collecting in this part of the world. With more collections from the Neotropics, the range of *C. fenyesi* will likely become more continuous. Strepitpeterans also often occur in small numbers. Small numbers, at any given time, may be a result of very short adult male life spans and may not necessarily reflect a scarcity of stylized hosts. Having very small males and parasitic adult females also cause them to be overlooked. However, the disjunct distribution found in Brazos County shows that the distribution may not be continuous throughout its range. The habitat preference of hosts of *C. fenyesi* may play an important role in determining the complete distribution pattern.

The geographic distribution of *C. fenyesi* does not coincide with the distribution of its only known host, *S. incerta*. The distribution of *S. incerta* and *C. fenyesi* overlap in the United States, except for a collection from southern Arizona. *S. incerta* also does not occur in the regions of Mexico, Central America, and parts of South America where *C. fenyesi* occurs. Thus, *C. fenyesi* must have a different host in these regions because *C. fenyesi* is a relatively weak flier and has a very short adult life (Cook 1996). This conclusion is noteworthy because most myrmecoid species are currently known from only 1 host, although most species have an unknown host association. It remains to be proven whether *C. fenyesi* has always had >1 male host, or if there has been a host switch in the United States. We feel that the most likely scenario is that a host switch occurred in the United States after the introduction of *S. incerta* (also noted by Kathirithamby and Hamilton 1985).

Several factors support the hypothesis of a recent host switch in the United States. First, for *C. fenyesi* to have been introduced with *S. incerta*, its females and males would have to have been introduced at the same time for them to establish and spread with *S. incerta*. This problem is further complicated by the dual hosts of *C. fenyesi* and the rapid spread of *S. incerta*. Given the dual host relationship of *C. fenyesi*, it is unlikely that the strepiterman parasite of *S. incerta* spread in all directions away from the point of introduction in such a short time. Finally, the western boundary of the range of *C. fenyesi* in North America is in an area of the United States (Arizona) where *S. incerta* is not known to occur. *Solenopsis geminata* and *S. xyloni* are likely candidates for the previous host of *C. fenyesi* in the United States because they have a biology that is relatively similar to *S. incerta* and are found within the known range of *C. fenyesi*. However, *C. fenyesi* has yet to be associated with *S. geminata* or *S. xyloni*. Therefore, we propose that a likely scenario is that
a host switch of male C. fengesi has occurred from a closely related native fire ant.

An alternative hypothesis to the above argument is that C. fengesi has a wider host range than is supposed. If this 2nd hypothesis is true, it is plausible that male C. fengesi might be, or is capable of, stylizing other species of fire ants, including several Solenopsis species found in South America.

Strepsipteran habitats are largely a function of their host habitat preference. Females of the family Myrmeccolacidae are parasitic throughout their development and adult lives. Male myrmeccolacids are parasitic throughout their development, but emerge for a very short free-living adult life. The adult lifespan is very short, ranging from a few hours to a few days (Kathirithamby 1989). The only other free-living stage is the triungulin, which leaves the female via a brood canal to the outside of its host. The triungulin is the stage that searches for its new host. Because of this relationship, strepsipterans have a distribution coinciding with that of their host. There is insufficient time for the adult male to establish and inhabit its own unique habitat, and a triungulin that is not in its future host’s habitat will not be successful in finding a host and will perish. The heterology of C. fengesi and other myrmeccolacids suggests that habitats with which they are associated should be an intersection of its dual host’s habitats.

We found no apparent distribution pattern within Brazos County. Fire ant colonies are abundant throughout the county, but the distribution of the host of the female, Heterothrix agitator Uhler (Cook 1996), is unknown. The spotty distribution of C. fengesi found in Brazos County is likely a reflection of female host distribution but could be the result of a recent host switch as proposed above. C. fengesi might still be expanding through its new host population.

Solenopsis invicta was found in all habitats surveyed in this study. The large S. invicta populations found at these collection sites should not be a limiting factor for levels of C. fengesi. Stylized S. invicta appear to be less common in grassland habitats. A chi-square test on pooled habitat data statistically supports this view. Significant differences between the grassland habitat and other habitats could be a result of the female host habitat or a different, unforeseen, limiting factor. This study shows that stylized S. invicta are not excluded from any of these habitat types.

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