Light trap capture of live Elenchus koebelei (Strepsiptera: Elenchidae)

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Abstract

Strepsiptera are a small order of obligately endoparasitic insects. Adult females are neotenic and never leave their host, instead bearing motile young that seek out their own insect hosts to infect. Males eclose without killing their hosts. In their 4-h adult lifespan, they fly off to search for mating opportunities, assisted by unconventional eyes with few, but large, ommatidia. Such distinctive features make Strepsiptera interesting in their own right, but also offer an opportunity to better understand evolutionary innovation. Unfortunately, Strepsiptera also are minute, reclusive, and difficult to obtain, severely reducing the study thereof, especially species not infecting solitary bees or social wasps. Here we describe methods for the successful capture of a strepsipteran species. We placed an ultraviolet light trap among Spartina alterniflora Loisel (Poaceae) shoots to attract adult male Elenchus koebelei Pierce (Strepsiptera: Elenchidae) in salt marshes in the southeastern United States. In 72 d of sampling, 488 adult males were captured between 30 min before and 15 min after sunrise. None arrived more than 63 min before or 36 min after sunrise. The majority of E. koebelei were caught at wind speeds ranging from 0 to 10 km/h; however, a light breeze of about 1.5 km/h appears to be preferred. The highest daily catches occurred when the temperature was between 23 and 26 °C. No Strepsiptera were caught at temperatures below 17 °C. With 521 adult male E. koebelei caught in a single light trap, our results show this little-known parasite may be reliably obtained, enhancing opportunities for further study.

Key Words: temperature; time; wind speed; Spartina alterniflora; twisted-wing parasite; crepuscular

Resumen

Strepsiptera es una pequeña orden de insectos endoparasitarios obligados. Las hembras adultas son neoténicas y nunca abandonan a su hospede- ro, sino que tienen jóvenes móviles que buscan a sus propios insectos hospederos para infectar. Los machos eclosionan sin matar a su hospedero. En su vida adulta de 4 horas, vuelan para buscar oportunidades de apareamiento, asistidos por ojos no convencionales con pocos, pero grandes, ommatidios. Tales características distintas hacen que Strepsiptera sean de interés por ellos mismos, pero también ofrecen una oportunidad para comprender mejor la innovación evolutiva. Desafortunadamente, los estrepsipteros también son pequeños, solitarios y difíciles de obtener, lo que reduce drásticamente el estudio de los mismos, especialmente las especies que no infectan a las abejas solitarias o a las avispas sociales. Aquí describimos métodos para la captura exitosa de un especie de Strepsiptera. Colocamos una trampa de luz ultravioleta entre los brotes de Spartina alterniflora Loisel (Cyperales: Poaceae) para atraer al macho adulto de Elenchus koebelei Pierce (Strepsiptera: Elenchidae) en las marismas del sureste de los Estados Unidos. En 72 días de muestreo, 488 machos adultos fueron capturados entre 30 minutos antes y 15 minutos después del amanecer. Ninguno llegó más de 63 minutos antes o 36 minutos después del amanecer. La mayoría de los E. koebelei fueron atrapados a velocidades de viento que van de 0 a 10 km/h; sin embargo, parece preferible una ligera brisa de aproximadamente 1.5 km/h. Las capturas diarias más altas ocurrieron cuando la temperatura estaba entre 23 y 26°C. No se capturaron los estrepsipteros a temperaturas inferiores a 17°C. Con 521 macho adultos de E. koebelei capturados en una sola trampa de luz, nuestros resultados muestran que este parásito poco conocido puede obtenerse de manera confiable, mejorando las oportunidades para un estudio posterior.

Palabras Clave: temperatura; hora; velocidad del viento; Spartina alterniflora; parásito de alas retorcidas; crepuscular

The order Strepsiptera consists entirely of obligate parasites of other insects [Strepsiptera: New Latin, from Greek strēpsi- = “twisted” and pteron = “wing”). The family Elenchidae parasitizes planthoppers (Homoptera: Delphacidae). Adult females have larviform bodies lacking wings, legs, and eyes, and never leave their host insect. They are neotenic, giving birth to motile male and female offspring that crawl and spring on plants and animals seeking suitable insect hosts to en- ter. Adult males have the eponymous “twisted” wings of this order. In search of mating opportunities, males emerge from their hosts and fly with the aid of unique eyes resembling tiny blackberries (Fig. 1). The male inseminates a portal on the cephalothorax of the female (Kathirithamby 1989), which in the case of Xenos peckii Kirby (Strepsiptera: Xenidae) is known to be protruded further forth from the living wasp host and inflated to increase perceptibility at times when males are apt to fly (Hrabar et al. 2014). The vast majority of knowledge about Strepsiptera pertains to diurnal species in the genus Xenos that infect Polistes (Hymenoptera: Vespidae) wasps. This paper introduces a black light technique to capture the crepuscular strepsipteran Elenchus koe- belei Pierce (Strepsiptera: Elenchidae). Insights into E. koebelei natural history and physiology based on the technique also are presented.

Typically, Strepsiptera mate only once (Hughes-Schrader 1924; Kathirithamby 1989), with evidence of the male dying very soon af- ter (Kathirithamby 1989). Many specifics of the life history of E. koe- belei remain unknown, but based on E. tenuicornis Kirby (Strepsiptera: Elenchidae), it is expected in summer, when development times are shortest, that after several weeks the female gives birth to about 1,500
from light trap by-catch (Green 1902; Meadows 1967; Shepard 1979), similar methods can be used to catch virtually any known crepuscular or nocturnal Strepsiptera.

Materials and Methods

It was expected that E. koebelei would be attracted to ultraviolet electromagnetic radiation from earlier work on X. peckii Strepsiptera ($\lambda_{max} = 346$ nm) (James et al. 2016). Accordingly, we designed and constructed portable light sources from a pair of 15 watt T8 UV lamps (diam: 2.54 cm; 1 in). One was a black light (BL); the other black light blue (BLB), using General Electric 35884 and 35885 GE F15T8 fluorescent tubes, respectively (45.72 cm; 18 in) (General Electric Corp., Fairfield, Connecticut, USA). Later, when collecting at Wakulla Beach, Florida, we replaced the original black light blue with a longer GE 10531 F40BLB, a 40 watt T12 black light blue (dia.: 3.81 cm; 1.5 in; length: 121.92 cm; 4 ft). All GE black lights have peak emittance at 368 nm (General Electric 2017), but black light lamps provide more visible light. This makes collecting easier, but may not be as attractive to Strepsiptera. General Electric T12 rapid start ballasts were used with all of the lamps. This likely increased the UV output of the T8 bulbs, at the anticipated cost of reduced lifespan. To provide waterproofing, silicon sealed PVC caps were placed over the wiring at the ends of each of the lamps. The lights were hung vertically atop a white sheet draped over a frame of PVC tubing, as shown in Figure 2. Batteries and ballast were protected by a plastic bucket that could rest on the ground at low tide, or be suspended from the trap by wire at high tide. Electrical contacts were soaked in undiluted white vinegar to remove saltwater-induced corrosion. A toothbrush also was used to help clean heavily corroded surfaces. By attaching shorter legs, the base of the frame could sit beneath the canopy of S. alterniflora. In the less dense Spartina of Wakulla Beach, this coupled with wetting the trap base greatly enhanced E. koebelei catch.

A Taylor 9840N Instant Read Digital Thermometer (Taylor, Oak Brook, Illinois, USA) was used to take local temperature measurements. Beginning in late 2015, a Kestrel 5500 Weather Meter (Kestrel-Meters.com, Minneapolis, Minnesota, USA) was used to record local wind speed, temperature, and humidity.

The custom light trap was used to collect E. koebelei Strepsiptera, where sweep netting in stands of S. alterniflora had revealed substantial numbers of stylopized Prokelisia marginata or P. dolus planthoppers. Strepsiptera were collected in late Aug through Sep, and a few d in Oct and Nov in 2013; in 2014, only in Oct; and in 2015, in Jul through early Aug (Table 1). The main collection sites were the north branch of Guana Tolomato Matanzas National Estuarine Research Reserve, also known as GTM Research Reserve (GTM) (30.0702°N, 81.3447°W), in St. John’s County, Florida, just off the Guana River near the Atlantic Coast, and Wakulla Beach (WB) (30.1050°N, 84.2616°W) in Wakulla County, Florida, on the Gulf of Mexico (Fig. 3).

Elenchus koebelei males that landed on the light trap were captured and placed into vials via an aspirator or a moistened fine-tipped paintbrush. After returning from a field site, author James identified species under a dissecting microscope by immobilizing captured insects with a FlyStuff Flypad (10.1 × 14 cm; 4.0 × 5.5 in) (Genesee Scientific Corp., San Diego, California, USA) connected to a CO$_2$ beer regulator paired with a paintball CO$_2$ tank. Use of a portable CO$_2$ cylinder (590 or 710 ml; 20 or 24 oz) allowed sample processing in unconventional laboratory settings. Tanks can be refilled inexpensively at scuba diving or paintball shops.

Sunrise is the most relevant timing event for animals that are active around dawn (matinal). Measuring time relative to sunrise allows capture times to be compared at different dates within a field season,
between different field seasons, and between separate sites. Although the length of twilight can change dramatically depending on latitude and the time of yr, in northern Florida the duration of civil twilight—the time before sunrise when artificial illumination is not necessary to clearly distinguish terrestrial objects—remained between 23 and 27 min through summer and fall, with an average length of 24:44 (min:s). The duration of nautical twilight—a phase of twilight preceding civil twilight, when artificial lighting is necessary for humans to see acceptably on moonless mornings, but the horizon is still distinct—over the same time period ranged between 27 and 33 min, with an average of 29:20 (min:s). Astronomical twilight ranged from 27 to 35 min, and averaged 28:53 (min:s). These averages correspond to the twilight times labeled in Figures 4 and 5.

Variation in the start and duration of collection times is documented in Table 2. Effective start and duration times were determined in 2013. That knowledge was exploited in subsequent seasons to reduce effort and increase catch. During each season an early start time and long duration was revisited, which reaffirmed the soundness of the more abbreviated schedules (Fig. 4). Due to processing limitations in 2015, the site often was abandoned even though additional Strepsiptera still could have been collected.

SPECIES IDENTIFICATION

There are several ways to identify adult male *E. koebelei* in the field, even if one has never seen a living Strepsiptera before. First, adult Strepsiptera are not skillful walkers. Because of this and their general frenetic nature, energetic adult males tend to use their wings to assist them in walking. The most telltale sign of an *E. koebelei* is the arc their vibrating wings sweep out. It is difficult to describe, but utterly unlike any other flapping pattern. Once seen, it is immediately identifiable. Second, when less energetic, *E. koebelei* often walk with their wings held together above the thorax. However, the wings swing from side-to-side when they step because their legs are specialized for grasping onto a female. Third, although *E. koebelei* are tiny, often their bifurcated antennae can be recognized. When walking, they are extended forward with the branches separated, as with *E. tenuicornis* (Hassan 1939). Initially, one may find it helpful to use a magnifying glass to assist with in-field identification, but after a few sightings it is normally much more efficient to proceed with the naked eye.

Results

We captured 521 adult male *Elenchus koebelei* using the mobile light trap: 284 from the Guana Tolomato Matanzas Research Reserve on the Atlantic, and 237 from Wakulla Beach on the Gulf of Mexico. These Strepsiptera were caught primarily in mid-Jul through Oct (Table 1). Male elenchids have a short adult lifespan of about 4 h (Cook 2014). Although some Strepsiptera were processed in the field, the remaining live specimens were vigorous at least 2 h after capture, allowing sufficient time for processing or experimentation in the lab.

In 2014, we were available to trap *E. koebelei* only from Oct to Nov, the latter portion of the field season in a yr in which cool temperatures arrived early. During the 3-yr study, no Strepsiptera were captured on 14 mornings (Fig. 6; Table 1), 11 of which occurred in 2014. Nonetheless, that yr was indispensable for determining the lowest temperature at which *E. koebelei* eclose (Fig. 7).

In 21 field days at Wakulla Beach, the number of live captures per day had a minimum of 0, a lower quartile of 0, a median of 1,
a third quartile of 15, a maximum of 60, and a total live catch of 225, with an approximately 62% chance of catching at least 1 live Strepsiptera each morning. However, without including results from 2014, the lower quartile, median, and third quartile improve to 1, 3, and 18, respectively, and the chance of catching a live male rises to 13 out of 17, about 76%. In 51 field days at Guana Tolomato Matanzas Research Reserve, the minimum number of *E. koebelei* captured live was 0, the lower quartile was 1, the median 3, the third quartile 6, the maximum was 23, and the total live catch was 207, with a 45 out of 51 (about 88%) chance of capturing at least 1 live eclosed male each morning. Without 2014, the lower quartile, median, and third quartile improve to 2, 3.5, and 6, respectively, with a 39 out of 40 (97.5%) chance of catching a live male on any sampling day. These values are based on the 432 *E. koebelei* that were collected alive (Strepsiptera can quickly dry out on hot ultraviolet lights and die just before collection), including those caught at unrecorded times.

Most (488 out of 521, about 94%) *E. koebelei* arrived at the apparatus between 30 min before and 15 min after sunrise, as shown in Figure 5. None were captured more than 63 min before sunrise, or

![Fig. 3. Collection sites: The north branch of the Guana Tolomato Matanzas National Estuarine Research Reserve in Saint John's County, near Florida's Atlantic Coast, and Wakulla Beach, on the Gulf Coast in Wakulla County. [Produced with assistance from Eco-Regions of Florida. Level IV Ecoregions graphic developed by the Watershed Monitoring Section, Division of Environmental Assessment and Restoration, Florida Department of Environmental Protection, Tallahassee, Florida. Sourced from Griffith et al. (2001). Adapted with permission.](image-url)
James & Strong: Light trap capture of live *Elenchus koebelei*

Apart from finding an area with visibly stylopized planthoppers, the most important determinants of sampling success are temperature (500 out of 521, about 96%, were caught at temperatures ranging from 21.7–26.1 °C; 71–79 °F), wind speed (485 out of 521, about 93%, were caught at wind speeds from 0–11.3 km/h; 0–7 mph), and timing (488 out of 521, about 94%, were captured from 30 min before to 15 min after sunrise).

**Discussion**

Having live Strepsiptera allows for experimentation and detailed investigation. We used a portable light trap to provide reliable access to live adult male *E. koebelei* during the species’ mating season. Because Strepsiptera are known to be caught in light traps, the same general approach should be applicable to any Strepsiptera that flies in low light. However, one must first determine where they are and when they are active.

**SUITABLE HABITAT**

Prerequisites to catching *E. koebelei* are persistent stands of *S. alterniflora*, the larger, the better, and an abundance of *Prokelisia marginata* or *P. dolus* planthoppers, or both at once. It is also very important that sweep netting yield positive results prior to attempting light trap collection. Before realizing the primacy of this qualification, we sampled without success at a few waterfront locations in Franklin and Wakulla counties, Florida in 2013. Sweep netting also helps one to know where to position a light trap. However, given the presence of visibly stylopized planthoppers, there is every reason to expect live
eclosed *E. koebelei* can be captured at a site. Finally, promising sites may be worth revisitation, because early in a season hosts may be infected without external indication. New locations may even be colonized in particularly productive years.

**DIEL ACTIVITY**

At the onset of this study, the active period of *E. koebelei* was unknown. We hypothesized that the species is crepuscular, given that:

1. Host activity patterns are important indicators of strepsipteran activity, and delphacid planthoppers, especially the brown planthopper, *Nilaparvata lugens* (Stål 1854) (Hemiptera: Delphacidae), are known to migrate at dusk or dawn (Pender 1994; Qi et al. 2014)

2. Muir (1906) found that all specimens of the closely related species, *E. tenuicornis*, that he reared out in Hawaii eclosed between sunrise and 7 AM. [Time reckoning precedes the introduction of Daylight Saving Time.]

**Table 2.** Catch statistics and variation in *Elenchus koebelei* sampling duration. On average, all Strepsiptera were caught within a 20 minute period each day at Guana Tolomato Matanzas National Estuarine Research Reserve (GTM), and in just over a half hour at Wakulla Beach (WB). Due to logistics and inclement weather, the 2014 field season began late and was curtailed (no specimens were collected from WB, and only a few from GTM). Both locations are coastal sites in Florida, GTM on the Atlantic, and WB on the Gulf.

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>Average start of sampling before sunrise (minutes ± SD)</th>
<th>Average minutes sampling</th>
<th>Average minutes until first catch</th>
<th>Absolute max and (average max minutes) between catches</th>
<th>Average minutes between first and last catch</th>
<th>Average minutes sampling after last catch</th>
</tr>
</thead>
<tbody>
<tr>
<td>2013</td>
<td>GTM</td>
<td>42 ± 17</td>
<td>81</td>
<td>21</td>
<td>32 (14)</td>
<td>19</td>
<td>33</td>
</tr>
<tr>
<td>2013</td>
<td>WB</td>
<td>59 ± 26</td>
<td>85</td>
<td>27</td>
<td>19 (13)</td>
<td>32</td>
<td>29</td>
</tr>
<tr>
<td>2014</td>
<td>GTM</td>
<td>48 ± 7</td>
<td>66</td>
<td>36</td>
<td>20 (14)</td>
<td>7</td>
<td>19</td>
</tr>
<tr>
<td>2014</td>
<td>WB</td>
<td>51 ± 14</td>
<td>49</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>2015</td>
<td>GTM</td>
<td>49 ± 8</td>
<td>55</td>
<td>24</td>
<td>32 (12)</td>
<td>19</td>
<td>11</td>
</tr>
</tbody>
</table>
3. Eclosed *E. koebelei* are not encountered in diurnal sweep netting, even when net mesh sizes are suitably small and the percentage of stylized hosts may approach 40% (Stiling et al. 1991b).

It is possible *E. koebelei* is diurnal. However, that is unlikely because on several mornings the final catch of the day occurred before sunrise (Fig. 4). In fact, more than 50 live *E. koebelei* were caught before daybreak on 2 separate mornings (Fig. 4; Supplemental data). Although the detectability of a light trap is reduced with increasing ambient light (particularly at distance), at Wakulla Beach we observed 2 additional peaks in captures that occurred from 10 to 15 min after sunrise, and from 20 to 25 min after sunrise, indicating that the trap was sufficiently conspicuous to attract *E. koebelei* well after sunrise. (This also indicates that the Strepstipitera did not have far to fly: at even moderate distances after sunrise, artificial light should fade into the background.) It is also possible *E. koebelei* is nocturnal. However, we conclude that is highly unlikely, given the brief lifespan of eclosed adult male Strepstipitera and that some specimens were captured over 30 min after sunrise.

Because *E. koebelei* are eclosed at dawn, they are visually capable of flying at dusk as well. However, on the windless evening of 27 Sep 2013, no *E. koebelei* were captured or sighted in sampling at Wakulla Beach, where the insects were known to be present. Sampling began 13 min before sunset and ended 70 min thereafter. On that evening, dragonflies were flying in great numbers, some as long as 28 min after sunset. Although their hunting success would decline sharply with increasing darkness, dragonflies likely pose a threat to Strepstipitera at dusk. It is unknown how the eyeless calling females would be aware of dragonflies at whatever density, or even the sighted males, before having cast off their pupal caps and therefore committing to eclosure. Judging from their treatment of other variable parameters such as moon illumination and tide height (see below), the strepsipteran approach appears to be to ignore them in favor of consistent factors. It is therefore most likely that adult *E. koebelei* are active only around dawn (i.e., strictly matinal), when most bats are finished feeding, and larger predatory insects are not yet active.

**OTHER CONDITIONS INFLUENCING CATCH**

Factors such as temperature, timing, wind speed, and the absence of precipitation, significantly influence *E. koebelei* catch. In this study, most data were collected and disseminated by area weather stations. Such records are not as accurate as local measurements, but are more readily available, are still very useful in determining sampling success, and provide data before arriving at a site, which can save a great deal of turmoil. Over the course of the study, a local thermomter was nearly always on hand. After 4 Aug 2015, a portable weather station also was available to record local wind speed, temperature, and humidity.

**TEMPERATURE**

The most productive temperature range for catching *E. koebelei* was found to be from 21.7 to 25.6 °C (71–78 °F), within which 93% of all *E. koebelei* were caught. This range also contained the most favorable ratios of catch to days at temperature. No *E. koebelei* were captured at temperatures below 17.2 °C (63 °F). *Elenchus koebelei* eclosed at the highest temperature encountered (27.8 °C [82 °F]); however, sampling efficiency declined sharply for temperatures above 25.6 °C (78 °F) (see Fig. 7.) Avoiding eclosing when it is warmer may help protect *E. koebelei* from attack by aerial predatory insects, which generally have higher take-off temperatures.

**TIMING**

We found it best to have the trap completely operational from 35 min before sunrise to about 15 min after sunrise at Guana Tolomato Matanzas National Estuarine Research Reserve, where strong breezes are rare. However, at Wakulla Beach, a windier site, sampling from 45 min before until 25 min after sunrise produced better results. These findings should generalize to other locations.

**WIND**

*Elenchus koebelei* are quite capable fliers, but they are minute and lightweight, so substantial local winds could blow them well off course, and also obscure the location of calling females. Furthermore, it is likely ‘strong’ wind is the predominant factor in patchy strepsipteran distribution. In the absence of a local wind meter, the Beaufort scale or the wind speed from an area weather report can be used. Wind speeds from about 1.6 to 9.7 km/h (1–6 mph) appear to be best (Fig. 8). Still air conditions were found to be good, and wind speeds from 9.7 to 12.9 km/h (6–8 mph) were suitable. *Elenchus koebelei* rarely flew at wind speeds above 16 km/h (10 mph). No Strepstipitera ever were captured when the trap’s collection sheet billowed enough to destabilize it. However, when stronger winds died down several min before dawn, males still eclosed and were caught. At Guana Tolomato Matanzas Research Reserve, wind speed was greatly reduced and regularized by nearby trees, and eclosed *E. koebelei* exhibited a smooth single-peaked distribution of catch times relative to sunrise. At Wakulla Beach, the frequency of windy conditions between sampling days greatly increased catch variance, while within sampling days, the prevalence of wind gusts likely prevented a unimodal distribution (Fig. 5).

For consistency, all analyses were done on wind data from area weather stations. However, those may overstate the wind speed in protected areas, such that still wind conditions could in fact yield the best results. Unfortunately, on-site wind speed data were available only for the last 7 d of trapping in 2015. Over that time period, they averaged 5.6 km/h (3.5 mph) less than area wind measurements, with 5 d registering 0 km/h (Supplemental data). To obtain a more in-depth treatment, wind speed should be monitored continuously and matched against individualized catch times.
Though very light drizzle was tolerated, *E. koebelei* were found to prefer mornings free of precipitation. Males appear to be highly sensitive to barometric pressure, such that they did not fly on mornings that seemed very promising, but suddenly degenerated into substantial rainfall. However, when rain was light enough to be of no concern for shorting out exposed electrical connections, it was also suitable for collecting *E. koebelei*.

*TIDE*

Tide height was found to be of little significance, particularly at Guana Tolomato Matanzas Research Reserve. It may increase the difficulty of collection, but does not appear to actually influence strepsipteran eclosion. There is some indication that the host insect, *P. marginata*, may avoid immersion, ostensibly to escape consumption by predatory fish. At Guana Tolomato Matanzas Research Reserve, the Pearson correlation coefficient between tide height and the number of *E. koebelei* caught was 0.12, with an estimated 62% chance of having arisen randomly. At Wakulla Beach, the correlation coefficient was −0.29 with an estimated 37% chance of having arisen randomly. However, when corrected for the range of water heights that occurred during collection episodes, the correlation coefficient fell to −0.02 (95%) and −0.21 (37%), respectively. The persistent slight negative correlation found at Wakulla Beach was due to the catch characteristics of the 2 extremely high yield days, and not due to consistent differential tide-based eclosing of male *E. koebelei*.

*Moonlight*

Only moon rise, moon set, and lunar visibility as a function of phase were recorded consistently. No data on cloud cover were noted regularly, and a light meter was not available to record relative brightness. However, within these confines, it was repeatedly found that *E. koebelei* did not eclose differently despite the greatly increased availability of light during full, and nearly full, moons. This lack of response suggests strongly that in addition to being completely blind, adult female *E. koebelei* also do not adjust their calling times on the basis of lunar light intensity.

Moonlight intensity does appear to influence catch, albeit negatively. That is, as found for other nonaquatic insects, the number of Strepsiptera eclosing ostensibly remains constant with respect to
moonlight, but on brightly moonlit nights the light trap has to contend with increased ambient light, and is therefore less efficient (Williams et al. 1956). Because \textit{E. koebelei} is crepuscular, the effect is less pronounced than what could be expected of nocturnal insects. However, it is worth noting that both cases of catches during astronomical twilight occurred on moonless nights.

\section*{LIGHT SENSITIVITY}

\textit{E. koebelei} were most often captured during twilight, the period between night and day when no sunlight reaches an observer directly, but sunlight redirected by the atmosphere still does (unlike at night). Twilight is divided into 3 formalized stages, based on the sensitivity of the human eye (timeanddate.com n.d.; US Naval Observatory 2011). However, despite this origin, the subdivisions also have relevance to \textit{E. koebelei}, as can be seen in Figures 4 and 5. In the morning, twilight begins at dawn and ends at sunrise. Astronomical twilight is the first stage of morning twilight; it occurs when the geometric center of the sun is between 18° (inclusive) and 12° (exclusive) below the horizon. At the beginning of astronomical twilight, the intensity of scattered sunlight is less than that from weak stars, and remains barely perceptible for a considerable interval thereafter (US Naval Observatory 2011). Throughout this stage of twilight the horizon is indistinct to a human observer. Nautical twilight occurs when the sun is between 12° and 6° below the horizon. It is named for nautical navigation by star and horizon sighting because in nautical twilight, the horizon remains discernible even on moonless nights, but most stars visible to the naked eye can be seen. In the absence of moonlight, during nautical twilight artificial illumination is required for most outdoor activities. Civil twilight occurs from when the sun is 6° below the horizon until sunrise. Under good atmospheric conditions in civil twilight, artificial illumination is not necessary to clearly distinguish terrestrial objects, and only the brightest celestial bodies can be seen by the naked human eye. Sunrise begins the moment any portion of the solar disk breaches the horizon.

At Guana Tolomato Matanzas Research Reserve, the largest number of \textit{Strepsiptera} were caught from 25 to 15 min before sunrise, the beginning of which roughly coincides with the onset of civil twilight. At Wakulla Beach, the majority of eclosed \textit{E. koebelei} were caught in 2 waves, the first from 30 to 25 min before sunrise, just prior to the start of civil twilight, and the second from 5 minutes before sunrise until sunrise itself, which marks the end of civil twilight (Fig. 5). Although the boundaries of twilight correspond to human visual sensitivity, it appears that civil twilight had strong bearing on the mating dynamics of both strepsipteran populations nonetheless, though at Wakulla Beach the preferred flight time may have been split to better coincide with troughs in wind activity. Unlike at Guana Tolomato Matanzas Research Reserve, the site at Wakulla Beach was not partially enclosed by trees, thus allowing for stronger winds and also greater ambient light intensity, either or both of which might have encouraged \textit{E. koebelei} to eclose at altered times. Accordingly, \textit{Strepsiptera} at Wakulla Beach were more apt to fly during nautical twilight, and only \textit{E. koebelei} at Wakulla Beach were found to fly during astronomical twilight (Table 3). Likewise, more \textit{E. koebelei} were collected after sunrise at Wakulla Beach than at Guana Tolomato Matanzas Research Reserve. This may be due to a post-dawn reduction in wind at the site.

The visual sensitivity of \textit{E. koebelei} has not been determined experimentally, but given these findings, we hypothesize that \textit{E. koebelei} see at roughly 1 twilight stage brighter than do humans, such that our astronomical twilight corresponds to their nautical twilight, human nautical twilight is the civil twilight of \textit{E. koebelei}, human civil twilight is their dawn, and full dawn and beyond may require significant internal shielding in \textit{E. koebelei}, which otherwise could adversely affect their visual acuity.

\begin{table}[h]
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\begin{tabular}{llll}
\hline
\textbf{Site} & \textbf{Male \textit{Elenchus koebelei} captured at known times} & \textbf{Number} & \textbf{Proportion} \\
\hline
\textit{GTM} & During astronomical twilight & 0 & 0.00 \\
 & During nautical twilight & 42 & 0.21 \\
 & During civil twilight & 123 & 0.62 \\
 & After sunrise & 34 & 0.17 \\
 & \textbf{Total} & \textbf{199} & \textbf{1.00} \\
\textit{WB} & During astronomical twilight & 7 & 0.04 \\
 & During nautical twilight & 66 & 0.34 \\
 & During civil twilight & 77 & 0.40 \\
 & After sunrise & 42 & 0.22 \\
 & \textbf{Total} & \textbf{192} & \textbf{1.00} \\
\hline
\end{tabular}
\caption{Adult male \textit{Elenchus koebelei} captured during different phases of morning. \textit{Elenchus koebelei} had a propensity to approach the light trap during civil twilight at both sites. However, because there are no nearby bordering trees, it is significantly windier and also brighter at Wakulla Beach (WB). These conditions appear to have extended acceptable flight times even into astronomical twilight at the site.}
\end{table}
WING EXPANSION

It typically took several minutes for any E. koebelei to visit the light trap regardless of when sampling began (Fig. 4). Furthermore, their wings are not fuelled as one would expect had they already been expanded within the pupal case, as is typical of male Strepsiptera. As a result, E. koebelei walk with wings held aloft. Because of these attributes, we hypothesize that E. koebelei do not fly immediately upon eclosing—unusual for Strepsiptera—but must first expand their wings in the manner of other flying insects, as Hassan (1939) reported of E. tenuicornis. It may be that during this time, E. koebelei can become fixated on a present light trap. If so, this would help explain the effectiveness of deploying the trap several minutes before the first Strepsiptera were expected (Fig. 4), and perhaps the unit’s strong appeal so long after sunrise, as well. One also wonders if this approach improves immediate flight performance, and what effect such a ‘trial period’ might have on vision.

On several occasions we noted that moving the trap a few meters revived flagging catch totals. This indicated that many E. koebelei did not have far to fly to arrive at the trap, yet despite their considerable flight velocity, it still took several minutes for the first of them to do so. Although the unaccounted-for time could have been occupied by mating, many captured E. koebelei had very noticeably distended abdomens. Because Strepsiptera do not feed as adults and may spend substantial time in a pharate state awaiting appropriate conditions, the distension was probably due to sperm reserves, indicating that the males had not yet mated. Additionally, the act of strepsipteran mating is unlikely to last long (Muir 1906) or to be repeated (Hughes-Schrader 1924). Furthermore, in at least 2 strepsipteran species it has been noted that males die just a few minutes after mating (Kathirithamby 1989; Beani et al. 2005), but our (presumably unmated) specimens normally survived for hours when allowed to do so.

RESISTANCE TO DROWNING

Unlike gnats, alate ants, and other flying insects attracted to the light trap, E. koebelei did not drown when water affixed their bodies to the trap’s support beams. This was discovered accidentally after a rainstorm, when the erected trap was carried through wet grass, and exploited thereafter. In stunted, less dense Spartina such as that at Wakulla Beach, attaching shorter legs to the trap to adjust for the reduced canopy height and wetting the trap base, together act as another means of ensnarement. Capturing Strepsiptera in this manner tended to ruin their remarkable wings, but did assist in obtaining larger numbers of live Strepsiptera at Wakulla Beach, particularly on the 2 mornings with the greatest live catch counts: 63 on 17 Sep 2013, and 57 on 22 Sep 2013 (57 and 51 caught live at known times, respectively).

Strepsiptera can survive at least 29 min in such conditions. This ability to avoid immersion asphyxiation may relate to the poorly understood strepsipteran “balloon gut” (Pohl & Beutel 2005; Beutel & Pohl 2006), or to the thinness of the strepsipteran cuticle, such that they may be able to breathe through it, as they ostensibly do as fully embedded larvae. The loss of all but 1 spiracle that has occurred in E. koebelei can become fixated on a present light trap. If so, this would help explain the effectiveness of deploying the trap several minutes before the first Strepsiptera were expected (Fig. 4), and perhaps the unit’s strong appeal so long after sunrise, as well. One also wonders if this approach improves immediate flight performance, and what effect such a ‘trial period’ might have on vision.

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