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Ad-hoc devised phototraps unravel *Cerambyx miles* diel activity in the wild (Coleoptera: Cerambycidae)

Luis M. TORRES-VILA*, F. Javier MENDIOLA-DÍAZ, Rafael LÓPEZ-CALVO, Francisco PONCE-ESCUERO, Álvaro SÁNCHEZ-GONZÁLEZ, Félix FERNÁNDEZ-MORENO

Servicio de Sanidad Vegetal, Consejería de Agricultura DRPyT, Junta de Extremadura, Avda. Luis Ramallo s/n, 06800 Mérida, Badajoz, Spain –
luismiguel.torres@juntaex.es; luismiguel.torresvila@gmail.com*Corresponding author; ORCID iD: <https://orcid.org/0000-0002-0650-6243>**Abstract**

Longhorn beetles are often categorized as diurnal, crepuscular or nocturnal depending on the diel (day-night) time window at which adults are active. A precise knowledge of the diel activity pattern in these species is essential to understand the selective forces involved in, and the adaptations resulting from, the evolution of circadian rhythms. The genus *Cerambyx* includes both diurnal and crepuscular/nocturnal species. In the case of *Cerambyx miles* Bonelli, 1812, a usually scarce and localised species, diel activity remains poorly understood. While for some authors this longhorn is diurnal, for others it is crepuscular/nocturnal. In order to resolve this historical discrepancy, we studied the diel activity of *C. miles* in the wild in 2020 and 2021 using ad hoc devised phototraps (with and without capture) and we examine to what extent our field results conformed to literature. Our data (n = 139 captures/sightings) show that about 94% of the activity of *C. miles* is diurnal, 5% crepuscular, and less than 1% nocturnal. Diel activity started at dawn, raised progressively during the morning, peaked in the late afternoon (17.00–20.00 h) and declined abruptly just before dusk. Our field results were not consistent with literature data (n = 103 diel activity records retrieved from 79 references), in which diel activity was scored as 60% diurnal, 26% crepuscular and 14% nocturnal. We argue possible causes involved in the literature bias and we discuss the diel activity of *C. miles* from a behavioural, ecological and evolutionary perspective.

Keywords: circadian rhythm, nycthemeral rhythm, diurnality, phototrapping, adaptive behaviour, literature bias.**Introduction**

Coleopterans in the family Cerambycidae, commonly called longhorn beetles due to their long and stylized antennae, are one of the most numerous groups of insects on earth, with some 38,000 species and more than 4,000 genera in 8–9 subfamilies (Bouchard et al. 2011; Nie et al. 2021; Tavakilian & Chevillotte 2022). The Cerambycinae subfamily, perhaps the most hyperdiverse and evolved among them, constitutes a monophyletic group comprising 11–12,000 species extremely variable in morphology and behaviour (Napp 1994; Hanks 1999; Rossa & Goczał 2021). Among their most striking biological features, there is an extreme variation in adult activity circadian rhythms (Hanks & Wang 2017), with light and temperature being major synchronizing agents or zeitgebers (Tomioka & Matsumoto 2010). Longhorn species are often categorized as diurnal, crepuscular or nocturnal depending on the diel (day-night) time window at which adults are active. A precise knowledge of the diel activity pattern in these species is essential to understand the selective forces involved in,

and the adaptations resulting from, the evolution of circadian rhythms (Suter & Benson 2014). Linsley (1962) even proposed dividing the Cerambycinae into two groups based on diel activity pattern.

Within the Cerambycinae, the type genus *Cerambyx* Linnaeus, 1758, includes 13 species occurring in the western Palaearctic realm, of which seven are present in Europe (Bense 1995; Danilevsky 2022; Fauna Europaea 2022) and four in Iberia, namely *C. cerdo* Linnaeus, 1758, *C. welensii* (Küster, 1845), *C. miles* Bonelli, 1812 and *C. scopoli* Fuessly, 1775 (Vives 2000; González-Peña et al. 2007). A noteworthy evolutionary aspect is that within the genus *Cerambyx* have evolved both strictly diurnal (*C. scopoli*) and mainly crepuscular/nocturnal species (*C. cerdo*, *C. welensii*), but the diel activity pattern of *C. miles* is unclear. While for some authors *C. miles* is crepuscular/nocturnal, for others it is a markedly diurnal species, flying in the central hours of the day in full sun, very often visiting flowers (see Torres-Vila & Echevarría-León 2019 for a mini-review). It is possible that *C. miles* is an ambivalent species, displaying both diurnal and nocturnal activity.

However, in most insect species there are precise diel activity periods linked to endogenous circadian rhythms – often coupled to photoperiod – (Tomioka & Matsumoto 2010; Beck 2012; Saunders 2012) rather than the diffuse diel activity reported for *C. miles*. Diel activity is viewed as the result of an adaptive process to maximise fitness in which selection pressures shaping species-specific physiology, morphology and behaviour differ markedly between diurnal and nocturnal species. Moreover, since adaptations to either night-time or day-time activity are expected to incur in significant energetic costs (somatic and reproductive), one could predict that a simultaneous adaptation to day and night lifestyles should be rare in nature. A fine adaptation to both light and dark regimens, in addition to being energetically costly in fitness terms, could even be somewhat morpho-physiologically incompatible, for instance, regarding compound eye size or ommatidia structure. In longhorn beetles specifically, eyes in nocturnal species are noticeably larger than in diurnal species and/or differ in the number of facets (Bilý & Mehl 1989); and also in diurnal species (especially those active under full sunshine) the peripheral rhabdomes of the ommatidia are smaller than in nocturnal species (Gokan & Hosobuchi 1979). In some nocturnal species intense light exposure during the day may even cause degradation of the photoreceptors, which need to be repaired at dusk (Suter & Benson 2014).

The goal of this paper was twofold: 1) to assess the diel activity of *C. miles* in the wild by means of phototrapping devices designed ad hoc for large longhorn beetles, and 2) to examine to what extent field experimental results conform to existing literature.

Material and methods

Study species

Cerambyx miles (Fig. S1) is a saproxylic and univoltine species flying in the summer season (June–August). The species has been recorded from a number of deciduous trees (Picard 1929; Villiers 1978; Bense 1995), but it mainly develops in oak species and exhibits a marked preference for deciduous/marcescent oaks in relation to evergreen oaks (Torres-Vila & Echevarría-León 2019; Torres-Vila et al. 2022). Adults are large-sized (about 25–45 mm, antennae excluded) and blackish brown in colour with a more or less reddish apical third. They show sexual size dimorphism, the body is slightly larger in females than in males while antennae are longer in males than in females. Mated females lay eggs in bark crevices and wounds of the host trees. After hatching, neonate larvae bore into the inner bark and initiate feeding subcortically. Larvae then tunnel increasingly wider and longer galleries into the sapwood and the heartwood. Larval development usually lasts 2–3 years and pupation occurs within a pupal cell in the sapwood in late summer. Pupal

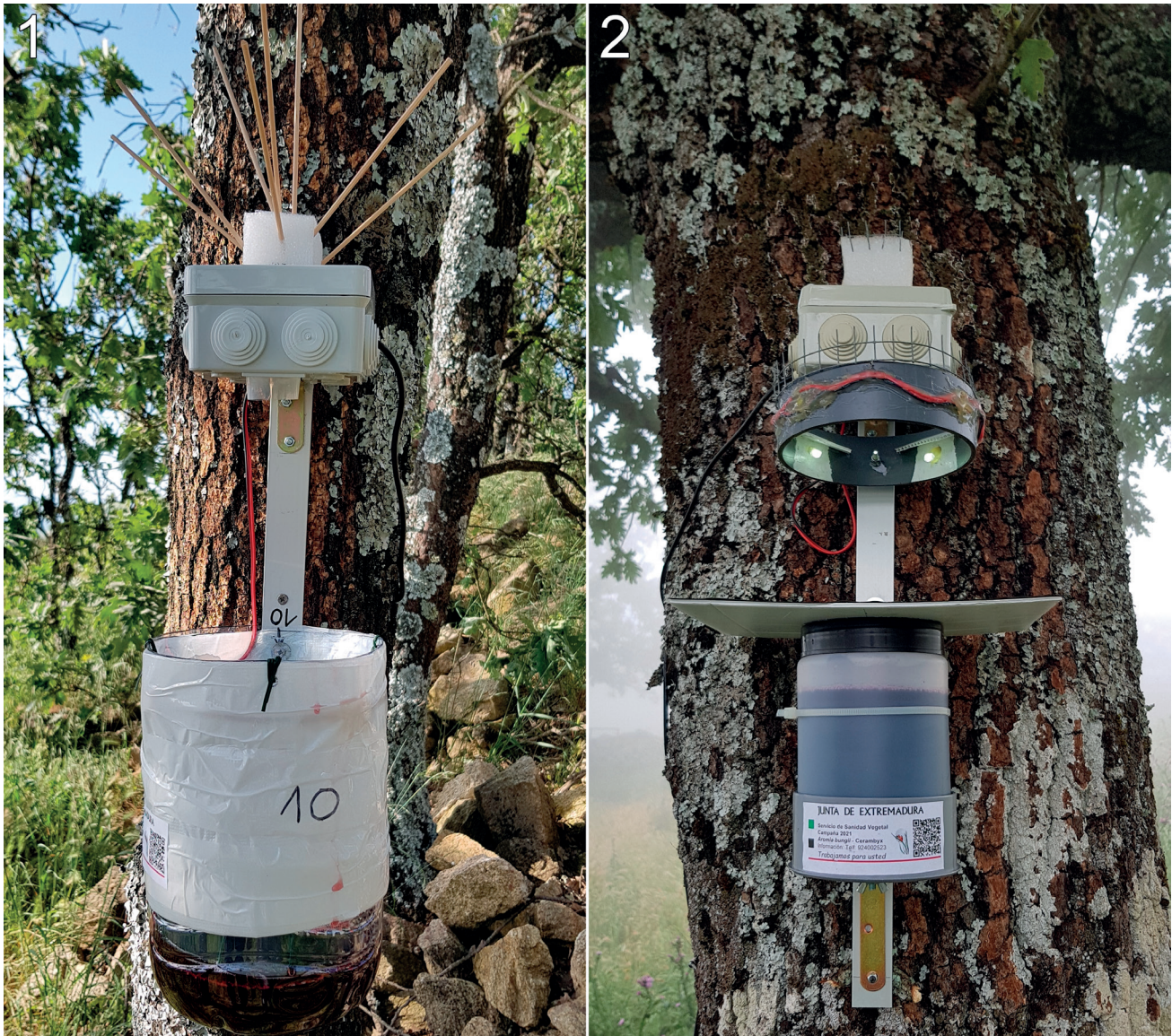
stage lasts about one month to complete and emerged adults overwinter in the pupal cell in a pre-reproductive stage until the late spring of the following year, when they leave the tree and reinitiate life cycle.

Cerambyx miles occurs in most Europe and the Caucasus (Danilevsky 2022; Fauna Europaea 2022). In the Iberian Peninsula has been reported in Spain and Portugal but unevenly. In Portugal the only known report corresponds to a historical record from Beja, in the lower Alentejo (De Oliveira 1882), while in Spain it is found in several regions especially in central and southern areas (Torres-Vila & Echevarría-León 2019). *Cerambyx miles* is usually a scarce and localised species, even if in some sites and years relatively abundant populations have been documented over its distribution range, including Romania (Săvulescu 1969), France (Micas 2010), Spain (Torres-Vila & Echevarría-León 2019) and North Macedonia (Cvetkovska-Gjorgjievska & Torres-Vila 2022). Some decades ago *C. miles* was even considered potentially harmful in some fruit trees. Currently, it is no longer viewed as a pest, unlike other congeneric species such as *Cerambyx dux* (Faldermann, 1837) with which *C. miles* was sometimes confused (Torres-Vila & Echevarría-León 2019 and references therein).

Phototraps: electronic components

We built an image capture device (ICD) developed ad hoc for *C. miles* and other large and medium-sized longhorn species, which was designed to work coupled to a food attractant. The ICD consists of: 1) a central processing unit (Raspberry Pi mod. A+) managed with Raspberry Pi OS v. 1.4 (formerly Raspbian), 2) a visible light camera (Raspberry Pi Camera Module v. 2.0), 3) a quartz clock installed in the Raspberry Pi GPIOs, and 4) a micro SD port with a 32 Gb memory card for the operating system and image storage. The ICD electronic components were arranged and protected within a watertight box (11 x 11 x 6 cm). A bottom hole (2 cm in diameter) was drilled in the box aligned with the digital camera objective, which was sealed with a glass and protected with a circular lens hood. To enable imaging at dusk/night, the ICD was provided with four light-emitting diodes (LED, 5 mm in diameter, clear white colour, 5000 °K, 5000 mcd, 25° aperture) disposed outside in the shape of a cross and oriented towards the image capture area. Lastly, due to the proximity of telephone/television antennas in some study sites (hill tops), the ICD was protected from potential electromagnetic radiations with a Faraday cage, custom made using a cardboard box lined with aluminium foil and waterproofed with adhesive tape.

The ICD was powered either by lithium batteries (three 5.5v, 20A LiPo units connected in parallel) or portable solar panels (12v, 10–15A, 38 x 32 cm) depending on trap location. Lithium batteries and solar panel accessories (charge regulator, 12v–7Ah valve-regulated lead-acid battery, 12v/5.5v transformer) were protected in a watertight



Figs 1-2 – Phototraps used in this study to assess the diel activity of *Cerambyx miles* in the wild; **1**, model PT1 with capture used in 2020; **2**, model PT2 without capture used in 2021. Both phototraps set in pyrenean oaks (*Quercus pyrenaica*) in the Montánchez mountain range, Cáceres, Extremadura (SW Spain). See text for a detailed description.

box (22 x 17 x 14 cm). The different elements (ICD, batteries, solar panels) were connected with USB/standard waterproof cables. A script was written with Raspberry Pi OS to take images at regular time intervals (see below) 24 hours a day, generating 3-5 Mb JPG files (labelled with the date, hour and minute of each shot) which were stored in the memory card. The LEDs turned on 5 seconds before each shot allowing digital camera to set optimal sensitivity and exposure time, and turned off when shot ended.

Phototraps: device and layout

We designed two phototrap models (PT1 and PT2) using the described ICD coupled to a food attractant. The PT1 model captured the adults (Fig. 1) whereas the PT2 model did not, letting them enter and leave the phototrap freely

(Fig. 2). The two phototrap models were designed to be placed in the trunk of host trees.

The PT1 model (Fig. 1) was assembled by mounting the ICD with an aluminium holder (3 x 30 mm section, 50 cm high) above a standard feeding trap (also called “tree trap”) as those previously described for the capture of other *Cerambyx* species (Torres-Vila et al. 2017). The feeding trap was made with a 5-l cylindrical PET container (a commercial water plastic bottle) in which the bottleneck was cut and replaced with a funnel made with a transparent semirigid acetate sheet (16 cm in diameter, hole 6 cm in diameter). A circular piece of 5-mm mesh rigid white plastic grid (15 cm in diameter), resting perimetally on a ring of the same material, was fixed 7 cm apart from the container bottom to prevent the captured adults from drowning in the bait. The



Figs 3-8 – Some selected images (unretouched, original frames) showing phototrapped adults of *Cerambyx miles*; **3**, a *C. miles* male prowling the container of a PT1 phototrap at 19.05 h. Two marked *C. welensii* adults are visible within the trap. Montánchez, Cáceres, 7 July 2020; **4**, a *C. miles* male lured by a PT1 phototrap at 19.15 h before being trapped. Montánchez, Cáceres, 8 July 2020; **5**, a mated pair of *C. miles* prowling a PT1 phototrap at 18.25 h. Two marked *C. cerdo* adults are visible within the trap. Note the removable cardboard panel to protect the container from direct sunlight. Montánchez, Cáceres, 8 July 2020; **6**, a *C. miles* female feeding in the drinker of a PT2 phototrap at 14.21 h. Montánchez, Cáceres, 29 June 2021; **7**, a mated pair of *C. miles* (while female feeds) in the platform of a PT2 phototrap at 17.56 h. Cancho Blanco, Zarza de Montánchez, Cáceres, 1 July 2021; and **8**, a *C. miles* male feeding in the drinker of a PT2 phototrap at 14.14 h. Montánchez, Cáceres, 29 July 2021 (Local time, GMT+2).

ICD height above the trap was adjusted so that the camera focused the grid and framed the container inner walls (Figs 3-5). The LEDs were fixed in the inside top of the container, just below the acetate funnel, directing the light towards the plastic grid, connections and cables being fastened to

the container outside and waterproofed with a hot melt glue gun. The container was lined externally with a white plastic sheet to increase brightness inside the trap and minimize light leaking outside (Fig. 1). The ICD script was set to take an image every 5 minutes. Because PT1 trapped the

adults, it provided both the number and capture time, so that upon checking the images could be compared with beetles captured in each trap. Some captured adults were marked and released to improve data input. Marks allowed to differentiate captured and recaptured adults to assess whether capture event could eventually modify adult performance and behaviour. Captured adults were taken to the laboratory, sexed and marked. A fine layer of waterproof pen white correction fluid (Tipp-ex®, BIC, Clichy, France) was applied (a rectangle of about $5 \times 10 \text{ mm}^2$) and after drying, adults were marked with correlative numbers written with a black permanent fine marker pen (Lumocolor, Staedtler, Nuremberg, Germany) (Torres-Vila et al. 2017). In practice we used a double-marking system, as the reference number was written twice in different positions on the elytra: *C. miles* one mark on each elytron, *C. cerdo* both marks on the right elytron and *C. welensii* both marks on the left elytron (data of the last two species not shown). Marked adults were released on the next day in the vicinity of the phototraps. A drawback detected with the PT1 model was that some images lacked sharpness when captured adults were stressed and/or interacted with each other and with those of the congeneric species *C. cerdo* and *C. welensii*, so we developed the following PT2 improved phototrap model.

The PT2 model (Fig. 2) was designed looking for a device that would attract adults without capturing them, providing a meal to retain them for the time necessary to take the photograph. In this way, image quality would be improved since photographed adults would be calm while eating. PT2 trap was built by replacing the container of the PT1 model with an observation platform made with a plastic plate (24 x 18 cm) lined on top with a black velvet self-adhesive PVC sheet (Aironfix®). The platform was fixed above a PE container (1 l volume, 15 cm high, 10 cm in diameter, screw-on wide-mouth cap) to be filled with food bait (see below), which in turn housed inside it a 0.25 l erlenmeyer flask with water. The flask pumped water through a Vileda® wick towards a circular drinking trough made of the same material (6 cm in diameter) impregnated with a saturated sugar solution and set in the centre of the platform (Figs 6-8). The drinking trough was covered concentrically with a smaller circular plastic plate (5 cm in diameter) to avoid excessive evaporation. The container released the bait volatiles through 13 circular holes (9 mm in diameter) drilled in the platform in the shape of a semicircle around the drinking trough. Holes were covered by a fine plastic mesh to prevent small insects from entering the container (Figs 6-8). The platform-container set was supported by a PVC cup-shaped anti-tip base fixed to the aluminium holder. The joints between platform, bait container, water vial and PVC base were made to be easily removed, allowing cleaning and refilling with bait or water. LEDs were fixed around a PVC ring (4 cm high, 14 cm in diameter), which was horizontally attached to the aluminium holder just below the ICD, directing the light

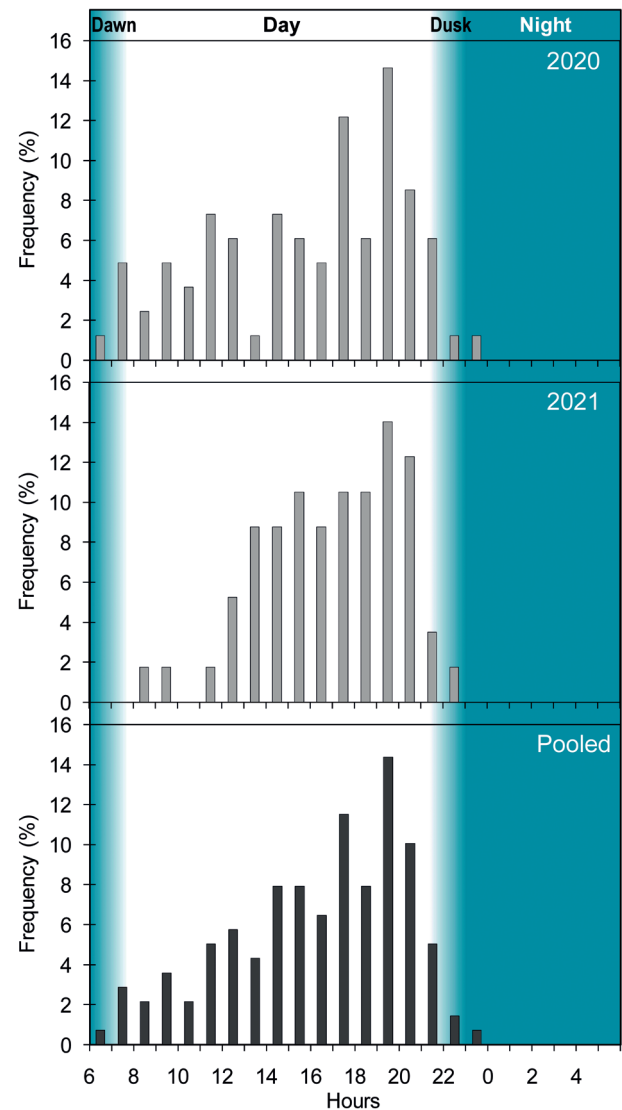


Fig. 9 – Diel activity (%) of *Cerambyx miles* in the wild during two consecutive years as assessed with phototrapping: frequency of captures in 2020 with PT1 traps (upper panel), frequency of sightings in 2021 with PT2 traps (central panel), and pooled data (bottom panel). The frequency distributions on an hourly basis show the strong prevalence of the diurnal behaviour exhibited by *C. miles* adults (Local time, GMT+2). Field trials were conducted both years during June-July at Montánchez mountain range, Cáceres (SW Spain). See text for additional details.

towards the platform (Fig. 2). The black platform increased the sharpness of the images and the velvet reduced light reflections. LED connections and cables were fastened to the ring outside and waterproofed with hot glue. Since the PT2 model did not capture adults, the ICD script was modified to take one image every minute to optimize the capture probability, since adult feeding time of *C. miles* observed in the laboratory is substantially longer (3-5 minutes or more). Note also that PT2 phototrap allowed to know the number of adults sighted rather than the number of adults captured, and so several sightings, on the same or successive days, could correspond to the same individuals.

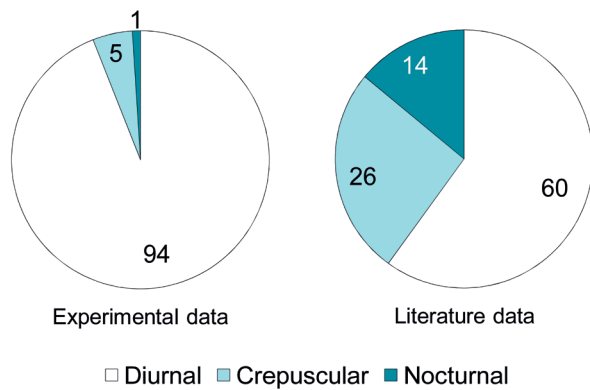


Fig. 10 – Pie charts depicting the diel activity (%) of *Cerambyx miles* depending on the data source, either field experimental data from this study (left) or literature data (right). Captures/sightings from this study ($n = 139$) and literature data ($n = 103$ records from 79 references, Table S1) were scored into three diel activity classes as either diurnal (D), crepuscular (C) or nocturnal (N). The two frequency distributions were significantly different (see text) suggesting an underlying bias in how entomologists have perceived or described the diel activity of *C. miles* adults.

Phototrap setting and follow-up

Each phototrap was fixed to the tree trunk with two small screws across the aluminium holder, so that the container edge (PT1) or the platform edge (PT2) were in close contact with the tree trunk to facilitate access of beetles, which reach the trap walking from the trunk (Figs 1-2). Phototraps were placed as vertical as possible at about 1.40-1.50 m height and in north aspect of the trees, to avoid excessive insolation. PT1 phototraps were protected when necessary with removable cardboard panels for shading in order to prevent container overheating (with captures inside) by occasional exposure to sunlight. Cardboard panels were adequately disposed in the tree trunk to not interfere with beetles walking towards the traps or with maintenance labours. Watertight boxes with batteries and electronic components were fixed at the base of the trees. Trap setting was completed by placing on the ICD top wooden skewers or a piece of wire mesh to prevent birds from perching. The bait used to lure the beetles was the same in both phototrap models. It consisted of a mixture of red wine, vinegar, commercial sugar, salt (2 l + 100 ml + 500 g + 500 g) and water to complete 5 l of solution. Trap containers were initially filled with fresh bait (0.5-1 l depending on trap model) and then regularly refilled to refresh fermenting bait and compensate for evaporation and degradation losses. Containers were completely emptied, cleaned and refilled with fresh bait when needed. During refilling operations, special care was taken that bait level never exceeds the antidrowning protective grid (PT1). Phototraps were inspected early in the morning, usually 2-3 times a week or daily at the peak of the flight period, and weekly at the beginning and end of beetle flight. Visits were used for collecting the catches (PT1), cleaning the container/platform, changing the drinker, refilling the bait/water and replacing the batteries and memory cards (maintenance operations depending on phototrap model).

Study sites and dates

Field trials were conducted from late May to late July for two consecutive years (2020 and 2021) in pyrenean oak forests (*Quercus pyrenaica* Willd.) located in the Montánchez mountain range, Cáceres, Extremadura (SW Spain). In 2020, we used three PT1 phototraps placed in Montánchez, Cáceres (39.2202N, 6.1368W). In 2021, we used four PT2 phototraps, two placed in Montánchez (39.2202N, 6.1368W) and two in Cancho Blanco, Zarza de Montánchez, Cáceres (39.2155N, 6.0363W). Experimental sites were selected because relatively abundant *C. miles* populations were known to occur from previous studies (Torres-Vila & Echevarría-León 2019).

Image and data processing

Images were viewed using Irfan View® free software, recording the metadata of the images (date, hour, site) in which *C. miles* adults were phototrapped. Given that the number of images to be processed was quite high (more than 10,000 per trap per week in 2021), JPG files from memory cards were recorded in solid hard disks to increase PC access speed and improve viewing, so that images could be managed as a video if necessary (e.g. seasonal or diel periods with no catches). Data of either capture time (PT1, 2020) or sighting time (PT2, 2021) for all phototrapped adults were scored into 24 one-hour periods, and frequencies of occurrence per hour were calculated prior to statistical analysis. We defined the three usual categories of diel activity (diurnal [D], crepuscular [C] and nocturnal [N]) based on sunlight intensity and human visual acuity rather than on a more formal definition of twilight depending on the angle of the centre of the sun below the horizon (0-6° civil twilight, 6-12° nautical twilight and 12-18° astronomical twilight), as the former criterion is more intuitive and practical, and the one implemented in historical and modern literature (Wakahara et al. 2018). In practice, we consider that, in our study site during June-July, the dusk twilight run from about 21.30 to 23.00 hours and the dawn twilight from 06.00 to 07.30 h, so that day (photophase) lasted from 07.30 to 21.30 h, and night (scotophase) from 23.00 to 06.00 h (all GMT + 2).

Reviewing literature data

In order to compare our field experimental results (phototrapping) with those from the entomological literature, we compiled all the published references we could find (including some personal communications) that provided useful information on the diel activity of *C. miles*. In addition to printed material, all available online resources and especially digital libraries were explored, including: BHL (<https://www.biodiversitylibrary.org>), Hathitrust (<http://www.hathitrust.org>), Zobodat (<https://www.zobodat.at>), Z-library (<https://z-lib.org>), Google Books (<https://books.google.com>), Google Scholar (<https://scholar.google.com>), RG (<https://www.researchgate.net>), Gallica-BNF (<https://gallica.bnf.fr>), BNE (<http://www.bne.es>), MDZ (<https://www.mdz.de>).

www.digitale-sammlungen.de/en) and e-rara (<https://e-rara.ch>). After a detailed reading of the original texts, the diel activity of *C. miles* was scored for each reference into one (or more when appropriate) of the three predefined diel activity periods: diurnal (D), crepuscular (C), and nocturnal (N) (Table S1). The time of collection was interpreted carefully as it does not necessarily indicate that the adult was active at that time. From these scores, the diel activity of *C. miles* based on literature records was quantified and analysed.

Statistical analyses

G-test was used to compare percentages/frequencies from field and literature data. Two-sample Kolmogorov-Smirnov test was used to compare frequency distributions of captures (unmarked adults) and recaptures (marked adults) in 2020, as well as the frequency distributions of captures/sightings between the two studied years (Sokal & Rohlf 1995).

Results

Field data

The two trap models were attractive, not only for *Cerambyx miles*, but also for *C. cerdo* and *C. welensii*, congeneric species that were also recorded both years in the two studied sites. Traps also showed to be highly effective (especially the PT2 model), since the series of images obtained allowed a correct specific identification in nearly all cases (> 99%).

In 2020 (PT1) and 2021 (PT2), 82 captures and 57 sightings of *C. miles* were recorded, respectively. A preliminary analysis showed no differences in diel activity between captures ($n = 65$) and recaptures ($n = 17$) in 2020 (Kolmogorov-Smirnov test, $D\text{-stat} = 0.25 < D\text{-crit} (0.05) = 0.37$, ns), so that both data sets were combined. The cumulative distributions of diel activity estimated either from captures in 2020 ($n = 82$) or sightings in 2021 ($n = 57$) were not significantly different (Kolmogorov-Smirnov test, $D\text{-stat} = 0.14 < D\text{-crit} (0.05) = 0.23$, ns), so the frequency distributions from both years were also pooled (Fig. 9). Lack of differences between both years occurred despite adult activity before noon tended to be somewhat higher in 2020 than in 2021, and that the curve was apparently smoother in 2021 than in 2020 (see discussion).

The activity of *C. miles* started timidly at dawn, raised progressively during the morning until reaching a maximum in the late afternoon (between 17.00 and 20.00 h), and then declined abruptly until it disappeared completely at dusk (Fig. 9). Out of all adults recorded ($n = 139$) only seven were observed during twilight periods (dawn/dusk) and just one was detected in the early night, between 23.00 and 00.00 h (Fig. 9). Consequently, field data clearly showed that *C. miles* exhibits a strong diurnal behaviour as about 94% of the activity was diurnal, 5% crepuscular, and less than 1% nocturnal (Fig. 10).

Literature data

Our literature search for records on the diel activity of *C. miles* adults yielded 79 references spanning a 178-year period (1845-2023). From these 79 references, 103 diel activity records were retrieved, which were classified in 62, 27 and 14 scores reporting diurnal, crepuscular or nocturnal activity, respectively (Table S1). Consequently, 60%, 26% and 14% of the activity was scored as diurnal, crepuscular and nocturnal, respectively (Fig. 10). Frequency distributions based on either field or literature data were significantly different (G-Test, $G = 45.85$, $df = 2$, $P < 0.001$), so that both datasets yielded quite inconsistent results regarding *C. miles* diel activity (Fig. 10).

Discussion

Our results obtained through phototrapping revealed that *C. miles* exhibits strong diurnality, extending its activity throughout the entire photophase, and especially from late afternoon to early evening (17.00-20.00 h). The activity of *C. miles* was very low during twilight (dawn and dusk) and almost residual during the scotophase (dark night). This suggests that the reduced lighting in the twilight windows (rising at dawn and decreasing at dusk) could act as a cue (either direct or indirect by adjusting the internal clock) to start or stop, respectively, *C. miles* diel activity. A major challenge in our study was to accurately differentiate live photographed specimens of *C. miles* from those of *C. cerdo* and *C. welensii*. In practice, the most useful diagnostic characters (some depending on sex) to assign species membership were: elytral sculpture, body shape, antennae length, thickness of antennal segments 3-5, length of antennal segment 11 and apex shape.

The diel activity pattern of *Cerambyx miles* was similar in 2020 and 2021, even if slight differences were observed between years, which were attributed to the research protocol and phototrap model used. First, the activity in the morning (09.00-12.00 h) was somewhat higher in 2020 (PT1) than in 2021 (PT2), which was explained in part because some marked adults in 2020 fell into the trap soon after being released. Second, the shape of the curve was more irregular in 2020 (captures in PT1) than in 2021 (sightings in PT2), which could be due to that successive sightings of the same specimens tended to smooth the curve in 2021. In fact, we observed in some males a marked trend to stay for long periods on the PT2 platform, as apparently they considered it as part of the tree trunk, and often exhibited territorial behaviour. It was also observed in 2020 (PT1) that some adults prowled but did not enter the traps, while others (especially small adults) managed to escape. Adult activity and behaviours recorded by phototrap were quite diverse and representative of *C. miles*' life in the wild, including: locomotion, resting, cleanliness, scouting, feeding, courtship, pair-bonding/mating, territoriality, male fighting, and even occasional wing spread.

Interestingly, the diel activity of *C. miles* observed in the field was not consistent at all with that inferred from literature reports. Literature data underestimated daytime activity by 34%, suggesting an underlying literature bias, which was visibly independent of geographical area or publication year. The occurrence of a great activity in the late afternoon and before dusk could explain why some entomologists misclassified *C. miles* as a crepuscular/nocturnal species. The underestimation of *C. miles* diurnal activity detected in the literature could be partly explained if: 1) dusk/night occasional reports have a higher proportional weight on a short 3-class diel activity scale (D/C/N) in comparison with the more precise one-hour 24-class scale used with phototrap, and 2) some references presumably categorise *C. miles* as crepuscular/nocturnal by wrongly assuming that its diel activity is similar to that of the large congeneric species (*C. cerdo* and *C. welensii*), a bias that would worsen if second-hand wrong information is reproduced in successive papers.

The common ancestor of cerambycids was likely crepuscular or nocturnal (Švácha & Lawrence 2014). However, numerous extant clades across the family evolved towards diurnality (Hanks & Wang 2017). Among the selection pressures that could have driven the adaptation to diurnality in cerambycids are avoid flying at night in cooler air temperatures and decrease the number of predators (Wakahara et al. 2018). A number of traits have proved to be (or are viewed as) the result of adaptations to diurnality in beetles, and some specifically in cerambycids. These include: body colour pattern (Linsley 1959; Săvulescu 1969; Švácha & Lawrence 2014; Monné et al. 2017), body size (Byrne & Dacke 2011; Hernández et al. 2011) eye size (Bílý & Mehl 1989), ommatidia structure and shape (Gokan & Hosobuchi 1979), antennae length (Švácha & Lawrence 2014) and even flight position, lifting or not the elytra when in flying (Kojima & Kato 2017). As a rule, nocturnal longhorns tend to have cryptic colorations, larger bodies, larger eyes, and longer antennae. Moreover, as crepuscular/nocturnal cerambycids are usually hidden during daytime, their antipredatory adaptations are generally mechanical as hardened sclerites, pilosity and spines (Švácha & Lawrence 2014).

As mentioned above, an interesting aspect is that within the genus *Cerambyx* both crepuscular/nocturnal (*C. cerdo*, *C. welensii*) and diurnal species (*C. scopoli*, *C. miles* –this study–) have evolved, implying that diel activity shifts have occurred within the genus along a more or less recent evolutionary time (Torres-Vila & Bonal 2019). Some of these saproxylic species live sympatrically in many forest contexts (Torres-Vila et al. 2017), so that how rigidly these longhorns partition their diel activity may have strong ecological and evolutionary consequences, because diel asynchrony can allow sympatric species that exploit the same niche to coexist syntopically (Suter & Benson 2014 and references therein). Moreover, sympatric cerambycid species often share dominant pheromone components, or even use pheromones of identical composition, so that differences in diel activity be-

tween species could be among the speciation mechanisms that serve to prevent interspecific attraction (Rice et al. 2020) and reproductive interference (Kyogoku 2015).

Conclusions

Our experimental results allow us to conclude that *C. miles* is a strongly diurnal species, thus clarifying the existing discrepancy in the entomological literature regarding its diel activity pattern. The selective pressures that have presumably driven this longhorn to diurnality and the species-specific functional adaptations to the diurnal lifestyle remain to be investigated, ideally in comparison to the nocturnal congeneric species.

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Supplementary material

Table S1 – An almost exhaustive list of references describing the diel activity of *Cerambyx miles* adults, scored in a three-class scale (D: Diurnal, C: Crepuscular, N: Nocturnal). Note that the same reference may provide more than one diel activity score. Relevant sentences from the original texts are also given. Also available at <https://www.researchgate.net/publication/371292424>

n°	Year	Reference	Diel activity ¹		Original text transcription • English translation
1	1845	De Serres, 1845		[C] N	les longicornes se divisent naturellement en deux tribus, les uns, en quelque sorte diurnes, volent uniquement pendant le jour, tandis que d'autres ne voltigent qu'après le coucher du soleil. On peut signaler parmi les genres nocturnes les ... <i>hammaticherus</i> [<i>C. cerdo</i> , <i>C. miles</i> , <i>C. welensii</i>] ... Les espèces à couleurs vives et brillantes appartiennent toutes à la première tribu; tels sont les vrais <i>cerambyx</i> ... • the longhorn beetles naturally divide into two tribes, some somehow diurnal, flying only during the day, while the others flying only after sunset. We can point out among the nocturnal genus the ... <i>Hammaticherus</i> [<i>C. cerdo</i> , <i>C. miles</i> , <i>C. welensii</i>] ... The brightly coloured and brilliant species all belong to the first tribe; these are the true <i>Cerambyx</i> ...
2	1849	Costa, 1849-1854		D	Gl'insetti perfetti sono diurni [<i>C. miles</i> , <i>C. cerdo</i> , <i>C. scopoli</i>] • Adult insects are diurnal [<i>C. miles</i> , <i>C. cerdo</i> , <i>C. scopoli</i>]
3	1870	Chenu, 1870		[D]	<i>Cerambyx</i> , Linné ... nos grandes espèces [<i>C. cerdo</i> , <i>C. miles</i> , <i>C. welensii</i> , <i>C. scopoli</i>] vivent sur les chênes, où elles recherchent le fluide qui découle des plaies de ces arbres, et, quand on veut les saisir, surtout lorsque le soleil est ardent, elles s'envolent avec facilité ou se laissent tomber de branche en branche • <i>Cerambyx</i> , Linné ... our large species [<i>C. cerdo</i> , <i>C. miles</i> , <i>C. welensii</i> , <i>C. scopoli</i>] live on oaks, where they seek the fluid which results from the wounds of these trees, and, when one wants to catch them, especially when the sun is blazing [at daytime], they fly away with ease or they drop themselves from branch to branch
4	1870	Millet de la Turtaudière, 1870		C	Les Cérambyx, connus généralement sous le nom de Capricornes, sont des insectes crépusculaires et de grande taille [<i>C. cerdo</i> , <i>C. miles</i>] • The <i>Cerambyx</i> , commonly known as Capricorns, are large, crepuscular insects [<i>C. cerdo</i> , <i>C. miles</i>]
5	1872	Lichtenstein, 1872		C	le <i>Cerambyx heros</i> Scop., ou le <i>Cerambyx miles</i> Bon., presque aussi communs l'un que l'autre: deux de nos plus grands insectes, que le vulgaire appelle des Capricornes, et qu'on voit souvent voler en été, au crépuscule • <i>Cerambyx heros</i> Scop., or <i>Cerambyx miles</i> Bon., one almost as common as the other: two of our largest insects, which the vulgar call Capricorns, and which are often seen flying in summer, at dusk

n°	Year	Reference	Diel activity ¹		Original text transcription • English translation
6	1881	Lucas, 1881		C	Le soir, un peu avant le coucher du soleil, on y voit de tous côtés ces Longicornes errer çà et là • In the evening, a little before sunset, we see these longhorns on all sides wandering here and there
7	1887	Guiliani, 1887		C	in compagnia del precedente [verso sera, <i>H. heros</i> Fabr.] • in the company of the previous one [towards evening, <i>H. heros</i> Fabr.]
8	1888	Heller, 1888		[D]	Entlang einer verfallenen Holzriese fing ich <i>Hammaticherus miles</i> Bon., [<i>H.</i>] <i>heros</i> Scopol., <i>Rosalia alpina</i> Linn. ... • Along a ruined wooden giant I caught <i>Hammaticherus miles</i> Bon., [<i>H.</i>] <i>heros</i> Scopol., <i>Rosalia alpina</i> Linn. ... [at daytime]
9	1889	Bedel, 1889		[C]	La plupart [des espèces du genre <i>Cerambyx</i>] ... ne sortent que par les soirs d'été • Most [<i>Cerambyx</i> species] ... come out only on summer evenings
10	1894	Xamheu, 1894		C [N]	c'est le soir, un peu avant le coucher du soleil, qu'il commence à apparaître • it is in the evening, a little before sunset, that it begins to appear
11	1895	Rertolini, 1895		D	ai Giardini • in the Gardens [at daytime]
12	1898	Marquet, 1898		[D]	sur les <i>Crataegus</i> / Pris une fois en quantité ... sur <i>Crataegus azarolus</i> • on <i>Crataegus</i> / Taken once in quantity ... on <i>Crataegus azarolus</i>
13	1898	Xamheu, 1898		D	En plein jour • In broad daylight
14	1906	Müller, 1906		D	in Eichenwäldchen bei Tage fliegend, ziemlich häufig • flying in oak forests by day, quite common
15	1906	Penecke & Müller, 1907		D	im niederen Eichengestrüpp rings um die Kekova jama und auf dem Glusac im Sonnenschein fliegend mehrere <i>Cerambyx miles</i> Bon. (darunter nicht ein [<i>C.</i>] <i>cerdo</i>) • in the lower oak thicket around the "Kekova Jama" and on the Glusac several <i>Cerambyx miles</i> Bon. flying under the sun (not including [<i>C.</i>] <i>cerdo</i>)
16	1909	Depoli, 1909		C	Verso sera trovai sugli aceri il <i>Rhopalopus insubricus</i> , [<i>R.</i>] <i>hungaricus</i> altrove assai raro, e sui pruni il bel <i>Clythantus speciosus</i> con la sua varietà coperta di polviscolo, detta <i>Ganglbaueri</i> , così pure il <i>Cerambyx miles</i> , [<i>C.</i>] <i>nodulosus</i> e le due specie del <i>Purpuricenus</i> • Towards evening we find on the maples the <i>Rhopalopus insubricus</i> , [<i>R.</i>] <i>hungaricus</i> very rare elsewhere, and on the prunus the beautiful <i>Clythantus speciosus</i> with its variety covered with dust, called <i>ganglbaueri</i> , as well as the <i>Cerambyx miles</i> , [<i>C.</i>] <i>nodulosus</i> and the two species of <i>Purpuricenus</i>
17	1922	Borg, 1922		D	These insects do not fly readily, except towards midday [referring to both <i>Cerambyx miles</i> L. and <i>Capnodis tenebrionis</i> L.]
18	1924	Planet, 1924		[D]	on l'observe à l'état adulte non seulement sur son arbre nourricier mais souvent aussi sur les fleurs de différents arbustes de la tribu des Rosacées: Amandiers, Aubépiniers et Azéroliers • it is observed in the adult stage not only on its host tree but often also on the flowers of different shrubs in the Rosaceae tribe: almonds [<i>Prunus</i>], hawthorns [<i>Crataegus</i>] and azaroles [<i>Crataegus azarolus</i>]
19	1928	Abot, 1928		[D]	Sur le chêne et aussi sur les [fleurs des] amandiers et le <i>Crataegus</i> • On oak and also on the [blossoms of] almond trees and <i>Crataegus</i>

n°	Year	Reference	Diel activity ¹			Original text transcription • English translation
20	1929	Picard, 1929	D			Sur les troncs d'arbres, ou au vol, parfois en plein soleil / Je l'ai vu voler, dans l'Hérault, en plein soleil, au-dessus des garrigues • On the trunks of trees, or in flight, sometimes in full sun / I saw it fly, in the Hérault, in full sun, above scrublands
21	1949	Müller, 1949-1953	D			L'adulto trovasi, oltre che sui tronchi, anche sui fiori delle piante nutritrici, oppure a volo in pieno sole • The adult can be found, as well as on the trunks, also on the flowers of the nourishing plants, or in flight in full sun
22	1955	Heyrovský, 1955	[D]			Imago často na květech chebdi (<i>Sambucus racemosa</i>) • Imago often on red elder flowers (<i>Sambucus racemosa</i>)
23	1957	Khnzorian, 1957	D	C		Взрослые особи встречаются днем на цветах чертополохов (<i>Echinops, Cirsium</i>) / Взрослые особи обычно летают в сумерки, но одну самку мы нашли до захода солнца (в 18 часов) на цветке зонтичного • Adults are found during the day on the flowers of thistles (<i>Echinops, Cirsium</i>) / Adults usually fly at dusk, but we found one female before sunset (at 18 h) on an umbrella flower
24	1957	Thurner, 1957	[D]	C		Gegen Abend im Flug • Towards evening in flight
25	1961	Della Beffa, 1961			N	[notturmo] • [nocturnal]
26	1961	Panin & Săvulescu, 1961	[D]			Imago pe flori de <i>Sambucus racemosa</i> • Imago on flowers of <i>Sambucus racemosa</i>
27	1964	Von Demelt & Schurmann, 1964	D			Fliegt auch bei Tage und besucht manchmal auch Blüten (<i>Sambucus ebulus</i>) • It also flies during the day and sometimes visits flowers (<i>Sambucus ebulus</i>)
28	1965	Novotný, 1965	D			<i>Cerambyx cerdo</i> L. finden wir bei voller Mittagssonne im Flug ins Fangnetz oder an Eichen. Später ist hier <i>Cerambyx miles</i> Bonelli ... • We caught <i>Cerambyx cerdo</i> L. in full midday sun with the catching net or on oak trees. Later <i>Cerambyx miles</i> Bonelli is here ...
29	1966	Von Demelt, 1966	D			In Istrien z. B. kommen in einem alten Quercetum gleich drei <i>Cerambyx</i> -Arten vor, nämlich <i>cerdo</i> , <i>miles</i> Bon. und <i>velutinus</i> Brullé. Man trifft dort bei Tage, allerdings mehr am Nachmittag, im hellen Sonnenschein nur <i>Cerambyx cerdo</i> und <i>miles</i> • In Istria, for example, three <i>Cerambyx</i> species occur in an old Quercetum, namely <i>cerdo</i> , <i>miles</i> Bon. and <i>velutinus</i> Brullé. During the day, but more so in the afternoon, in bright sunshine, only <i>Cerambyx cerdo</i> and [<i>C.</i>] <i>miles</i> can be found there
30	1966	Mal, 1966	D			Par temps orageux, sur les troncs moussus de certains de ces arbres j'ai capturé quantité de <i>Cerambyx miles</i> Bon, <i>Scopolii</i> Fuers [sic], <i>Potosia mario</i> F., <i>Cetonia aurata</i> L. ... Certains de ces troncs fourmillaient littéralement de ces Insectes venus là pour se désaltérer de l'eau de pluie dégoulinant sur la mousse des écorces • In stormy weather, on the mossy trunks of some trees I caught plenty of <i>Cerambyx miles</i> Bon, [<i>C.</i>] <i>scopolii</i> Fuers [sic], <i>Potosia mario</i> F., <i>Cetonia aurata</i> L. ... Some of these trunks were literally swarming with these insects that had come there to quench their thirst from the rainwater dripping on the moss of the bark
31	1969	Mal, 1969	D			Je crois utile de signaler la capture d'un <i>Cerambyx miles</i> Bon. ... Le 4 juillet 1968 vers 15 heures, sur la route qui conduit à Riboux (Var) mon attention fut attirée par un longicorne noirâtre accroché à une plante basse ... un ♂ de <i>C. miles</i> • I believe it is useful to report the capture of a <i>Cerambyx miles</i> Bon. ... On July 4, 1968 around 15 h, on the road that leads to Riboux (Var) my attention was drawn by a blackish longhorn beetle clinging to a low plant ... a ♂ <i>C. miles</i>
n°	Year	Reference	Diel activity ¹			Original text transcription • English translation
32	1969	Săvulescu, 1969	D	[C]	[N]	... am putut observa masculi ceva mai vioi și chiar zburînd de la o tufă la alta, fără să se înalțe însă la mai mult de un metru / Se afirmă de asemenea că imago-ul poate fi găsit pe flori de <i>Sambucus racemosa</i> ; nu ne putem explica această afirmație decât ca un caz cu totul întâmplător. Faptul că specia are o oarecare activitate diurnă și că nu este atrasă de lumina artificială nu dovedește că este diurnă, anumite particularități în comportamentul indivizilor ne determină să credem că o activitate crepusculară sau chiar nocturnă nu este exclusă • ... I could see males a little more lively and even flying from one bush to another [at daytime], but without rising more than a meter / It is also stated that the imago can be found on the flowers of <i>Sambucus racemosa</i> ; we can only explain this statement as a case in point. The fact that the species has some diurnal activity and that it is not attracted to artificial light does not prove that it is diurnal, certain peculiarities in the behaviour of individuals lead us to believe that a crepuscular or even nocturnal activity is not excluded
33	1970	Colas, 1970	D			<i>Cerambyx miles</i> Bon. Deux exemplaires vers 16 heures • <i>Cerambyx miles</i> Bon. Two individuals around 16 h
34	1972	Colas, 1972	[D]			le <i>Cerambyx miles</i> , le plus abondant, est ... le plus gourmand. En août ou en juillet il a un «faible» pour les pêches tombées à terre. Il est connu en Provence sous le nom charmant de «mangepoires». Il aime aussi les pêches bien mûres et on le trouve la tête littéralement plongée dans le fruit [pendant la journée] • <i>Cerambyx miles</i> , the most abundant, is ... the most gourmand. In August or July it has a weakness for fallen peaches. It is known in Provence under the charming name of «mangepoires» ["pear-eater"]. It also likes very ripe peaches and we find it with the head literally buried in the fruit [during the day]
35	1972	Massa & Mignani, 1972			N	<i>Cerambyx miles</i> ... Essa è presente anche in Sicilia: una ♀ è stata infatti raccolta nottetempo, attirata dalla luce • <i>Cerambyx miles</i> ... It is also present in Sicily: a ♀ was in fact collected at night, attracted by [artificial] light
36	1973	Allenspach, 1973	D	[C]	N	Käfer nächtlich an Stämmen laufend oder fliegend. Schwärmen aber nicht selten auch tagsüber im hellen Sonnenschein • Beetles walking or flying on trunks at night. But it is not uncommon for them to swarm during the day in bright sunshine
37	1973	Dauguet & Dauguet, 1973	D			parfois au vol en fin d'après-midi, ou marchant à terre entre 17 et 19 heures • sometimes flying in the late afternoon, or walking between 17 and 19 h
38	1973	Mikšić & Georgijević, 1973	D			Bionomija: Imago leti danju • Bionomy: Imago flies during the day
39	1974	Hellrigl, 1974	D			Käfer Juni/August, fliegen bei Tag und besuchen auch Strauchblüten • Beetles June/August, fly during the day and also visit shrub flowers
40	1978	Villiers, 1978	D			Adultes sur les troncs d'arbres ou les fruits mûrs, volant souvent en plein soleil • Adults on tree trunks or ripe fruits, often flying in full sun
41	1978	Willemstein, 1978	[D]			[The author reports the following flowering plants visited by <i>C. miles</i> adults: <i>Sambucus racemosa</i> , <i>Crataegus</i> , <i>Mespilus</i> , <i>Prunus triloba</i>]
42	1985	Danilevsky & Miroshnikov, 1985	[D]			посещают цветы • [adults] visit flowers
43	1985	Neumann, 1985	D			Die Tiere fliegen tagsüber und besuchen auch Strauchblüten (besonders <i>Sambucus racemosa</i>) • The animals fly during the day and also visit shrub flowers (especially <i>Sambucus racemosa</i>)

nº	Year	Reference	Diel activity ¹			Original text transcription • English translation
44	1985	Vives, 1985		[C]		Los adultos poseen los mismos hábitos que las especies anteriores [<i>C. welensii</i> y <i>C. cerdo</i> , crepusculares] • Adults have the same habits as the previous species [<i>C. welensii</i> and <i>C. cerdo</i> , crepuscular]
45	1987	Mihály, 1987	D	C		Életmódja hasonló a nagy hörcsincéréhez • Its lifestyle is similar to that of the great capricorn beetle [on the trunks of trees during the day, sometimes flying around tree trunks in the afternoon, but mostly in the evening]
46	1990	Ferrero, 1990	[D]			Contrairement aux adultes des autres espèces [de <i>Cerambyx</i>], ceux du <i>C. miles</i> butinent les fleurs de diverses rosacées arborescentes • Unlike the adults of the other [<i>Cerambyx</i>] species, those of <i>C. miles</i> forage on the flowers of various arborescent rosaceae
47	1990	Plaza, 1990	D			Con frecuencia se ha escrito sobre las "supuestas" costumbres crepusculares de esta especie ... los ejemplares de ésta presentan una gran actividad diurna e incluso en las horas de mayor radiación solar, realizando todas su funciones vitales, pero nunca al crepúsculo o la noche • Frequently it has been written about the "supposed" crepuscular habits of this species ... the adults of this species present a great diurnal activity and even in the hours of greatest solar radiation, carrying out all their vital functions, but never at dusk or at night
48	1993	De Castro & Blanco, 1993		[C]	[N]	Los adultos ... son atraídos por la luz [artificial] [nocturnos] • Adults ... are attracted to [artificial] light [nocturnal]
49	1994	Pesarini & Sabbadini, 1994	[D]			L'adulto, attivo soprattutto d'estate, ha costumi molto variati: si può rinvenire infatti sul tronco o fra il fogliame delle piante ospiti, su frutta marcescente e su diversi fiori • The adult, active above all in summer, has very varied habits: in fact, it can be found on the trunk or among the foliage of the host plants, on overripe fruit and on various flowers
50	1995	Bense, 1995	D			found on the host-trees and on flowers, active in the daytime
51	1996	Echevarría & Echevarría, 1996	D			siempre en vuelo a horas de máxima insolación • always in flight at hours of maximum sunshine
52	1998	Sláma, 1998	D	C	N	Večerní a noční druh, ale imága se často i ve dne pohybuje po kmenech, někdy i létají. Heyrovský uvádí výskyt imág často na květech <i>Sambucus racemosa</i> . V Evropě jsem tento druh na květech nikdy nenašel, ale na Blízkém východě jsem ho nacházel na květech <i>Sorbus</i> • Evening and nocturnal species, but imagoes often move through the trunks during the day, sometimes even flying. Heyrovsky reports the occurrence of imagoes often on the flowers of <i>Sambucus racemosa</i> . I have never found this species on flowers in Europe, but in the Middle East I have found it on flowers of <i>Sorbus</i>
53	1999	Sparacio, 1999	D	C		Adulto di solito crepuscolare, ma attivo anche di giorno, sui vecchi tronchi e attirato dalla frutta matura • Adult usually crepuscular, but also active during the day, on old trunks and attracted by ripe fruits
54	1999	Sudre et al., 1999	[D]	C		au crépuscule autour des chênes verts / pris une fois en quantité sur <i>Crataegus azarolus</i> • at dusk around the holm oaks / taken once in quantity on <i>Crataegus azarolus</i> [at daytime]
55	2000	Barreda & Navarro, 2000	D			parece presentar una mayor actividad en las horas de máxima luz solar en que realiza gran número de vuelos • it seems to present a greater activity in the hours of maximum sunlight in which it makes a large number of flights
nº	Year	Reference	Diel activity ¹			Original text transcription • English translation
56	2000	Vives, 2000	D			Los adultos ... vuelan a pleno sol y no suelen acudir a las flores • Adults ... fly in full sun and do not usually go to flowers
57	2001	Vives, 2001	[D]	C		Son de actividad crepuscular pero algunas veces suelen acudir a las flores del género <i>Rhamnus</i> u otras umbelíferas [sic]. No suelen ser atraídos por la luz UV • They are crepuscular in activity but sometimes they tend to go to the flowers of the genus <i>Rhamnus</i> or other umbelliferae [sic]. They are not usually attracted to UV light
58	2004	Murria & Murria, 2004	D			por el día y en las horas de mayor insolación • during the day and during the hours of greatest insolation
59	2004	Verdugo, 2004		C		los hábitos de los adultos son igualmente crepusculares • adult habits are equally crepuscular
60	2006	Brelih et al., 2006	D			Imagoes active during the day, when keeping close to their foodplants and blossoming bushes, largely on Red Elderberry (<i>Sambucus racemosa</i>), feeding on pollen
61	2007	González-Peña et al., 2007		C		Como sus congéneres es de costumbres crepusculares • Like its congeners, it is of crepuscular habits
62	2009	Allemand et al., 2009	D		[N]	Adultes diurnes ... floricoles ... et polliniphages. Attirés par les lumières • Diurnal ... anthophyllous ... and pollinophagous adults. Attracted by [artificial] lights
63	2009	Bartenev, 2009	[D]			Жуки встречаются на цветках • Beetles are found on flowers
64	2009	Miroshnikov, 2009	[D]			Жуки летают в июне – августе, посещают цветы, в частности, зонтичных • Beetles fly in June-August, visit flowers, in particular, umbrellas
65	2010	La Mantia et al., 2010	D	C		Biology similar to previous species [<i>C. cerdo</i> , daytime and twilight activities on oaks]
66	2011	Gouverneur & Guérard, 2011			[N]	Attiré par les pièges à appât et la lumière • Attracted to baited traps and to [artificial] light
67	2012	ARER, 2012	D	C	N	L'adulto è attivo tra giugno e inizio agosto e lo si può rinvenire su tronchi, tra il fogliame delle piante ospiti, su frutta matura e su diversi fiori. Ha attività crepuscolare e notturna ma vola anche in pieno giorno • The adult is active between June and early August and can be found on trunks, among the foliage of host plants, on ripe fruits and on various flowers. It has crepuscular and nocturnal activity but also flies in broad daylight
68	2013	Siering, 2013	D			zur Mittagszeit (!); mehrere Tiere z.T. verpaart auf dem Boden und im trockenen Eichenlaub umherlaufend; 1 Männchen schwärmend; 28.06.13 • at lunchtime (!); several animals partly paired on the ground and walking around on the dry oak leaves; 1 male swarming; 28.06.13
69	2014	Gidei & Popescu, 2014	D			Adultii sunt diurni, fiind întâlniți în iunie-iulie pe inflorescențele de <i>Sambucus racemosa</i> • Adults are diurnal, being found in June-July on <i>Sambucus racemosa</i> inflorescences
70	2015	Grottolo & Pedersoli, 2015	D	C	N	Attività dell'adulto: diurna, crepuscolare e notturna; frequenta i fiori, ma si riscontra anche sui tronchi delle piante ospiti • Adult activity: diurnal, crepuscular and nocturnal; it frequents the flowers, but is also found on the trunks of the host plants

nº	Year	Reference	Diel activity ¹			Original text transcription • English translation
71	2016	Lara-Ruiz, 2016; Lara Ruiz J., per. comm. 2023	D			[Avistamientos durante el día en las siguientes especies de plantas:] • [Sightings during the day in the following plant species:] Caprifoliaceae: <i>Sambucus nigra</i> , <i>Virburnum opulus</i> ; Cistaceae: <i>Cistus albidus</i> , <i>Cistus clusii</i> , <i>Cistus ladanifer</i> , <i>Cistus laurifolius</i> , <i>Cistus monspeliensis</i> , <i>Cistus salvifolius</i> , <i>Fumana baetica</i> , <i>Fumana ericoides</i> , <i>Fumana ericifolia</i> , <i>Fumana laevipes</i> , <i>Fumana paradoxa</i> , <i>Fumana scoparia</i> , <i>Fumana thymifolia</i> , <i>Halimium atricarpifolium</i> , <i>Helianthemum asperum</i> , <i>Helianthemum canum</i> , <i>Helianthemum cinereum</i> ssp. <i>rotundifolium</i> , <i>Helianthemum hirtum</i> , <i>Helianthemum ledifolium</i> , <i>Helianthemum salicifolium</i> , <i>Helianthemum syriacum</i> , <i>Helianthemum villosum</i> ; Compositae: <i>Aster pilosus</i> , <i>Calendula arvensis</i> , <i>Carduus nutans</i> , <i>Centaurea scabiosa</i> , <i>Cichorium intybus</i> , <i>Cirsium acaulon</i> , <i>Eupatorium cannabinum</i> ssp. <i>cannabinum</i> , <i>Hieracium pilosella</i> , <i>Silybum marianum</i> , <i>Solidago canadensis</i> , <i>Taraxacum officinale</i> ; Rosaceae: <i>Crataegus monogyna</i> , <i>Filipendula ulmaria</i> , <i>Prunus spinosa</i> , <i>Rubus ulmifolius</i> , <i>Sorbus acuparia</i> ; Umbelliferae: <i>Aegopodium podagraria</i> , <i>Anthriscus sylvestris</i> , <i>Daucus carota</i> , <i>Eryngium campestre</i> , <i>Foeniculum vulgare</i> , <i>Heracleum sphondylium</i> , <i>Pastinaca sativa</i> ssp. <i>sylvestris</i>
72	2019	Torres-Vila & Echevarría-León, 2019	D			... controversia en relación al comportamiento circadiano y alimenticio de los adultos. Mientras que para algunos autores <i>C. miles</i> es crepuscular o nocturno ... la mayoría refieren que es diurno y vuela incluso a pleno sol en las horas centrales del día / Curiosamente, los adultos de <i>C. miles</i> tienen los ojos relativamente pequeños ... un carácter morfológico que podría estar relacionado adaptativamente con sus hábitos diurnos • ... controversy regarding the circadian and feeding behaviour of adults. While for some authors <i>C. miles</i> is crepuscular or nocturnal ... most report that it is diurnal and flies even in full sun in the middle of the day / Interestingly, the adults of <i>C. miles</i> have relatively small eyes ... a morphological character that could be adaptively related to their diurnal habits
73	2019	Touroult <i>et al.</i> , 2019			N	Adulte nocturne surtout observé par la technique du piège alimentaire • Nocturnal adult mainly observed by the food trapping technique
74	2021	Mpamnaras A.G., per. comm. 2021	D			[Field observations]: diurnal (Greece)
75	2021	Olmos-Jiménez C., per. comm. 2021	D			[Observaciones de campo]: tres ejemplares ... en inflorescencias de <i>Centaurea solstitialis</i> L. a pleno sol de mediodía ... en El Tiemblo (Ávila) • [Field observations]: three specimens ... on inflorescences of <i>Centaurea solstitialis</i> L. in full midday sun ... in El Tiemblo (Ávila) [Spain]
76	2021	Sláma M., per. comm. 2021	D	C		[Field observations]: I found imagoes mostly in the daytime randomly on fruit trees, never on flowers, little at dusk
77	2022	IUCN, 2022	D			The adult is diurnal
78	2022	MNHN-OFB, 2022			C	L'adulte est crépusculaire et se trouve sur les troncs des arbres-hôtes • The adult is crepuscular and is found on the trunks of host trees
79	2022	Sláma, 2022	D	C	N	Večerní a noční druh, ale imaga se často i ve dne pohybují po kmenech, někdy i létají • Crepuscular and nocturnal species, but the imagoes often move around the trunks during the day, sometimes even flying
Total scores			62	27	14	
Grand Total scores			103			

¹Diel activity scores, D: Diurnal, C: Crepuscular, N: Nocturnal. Those scores implicit to, or inferred from, the original texts are given in square brackets.

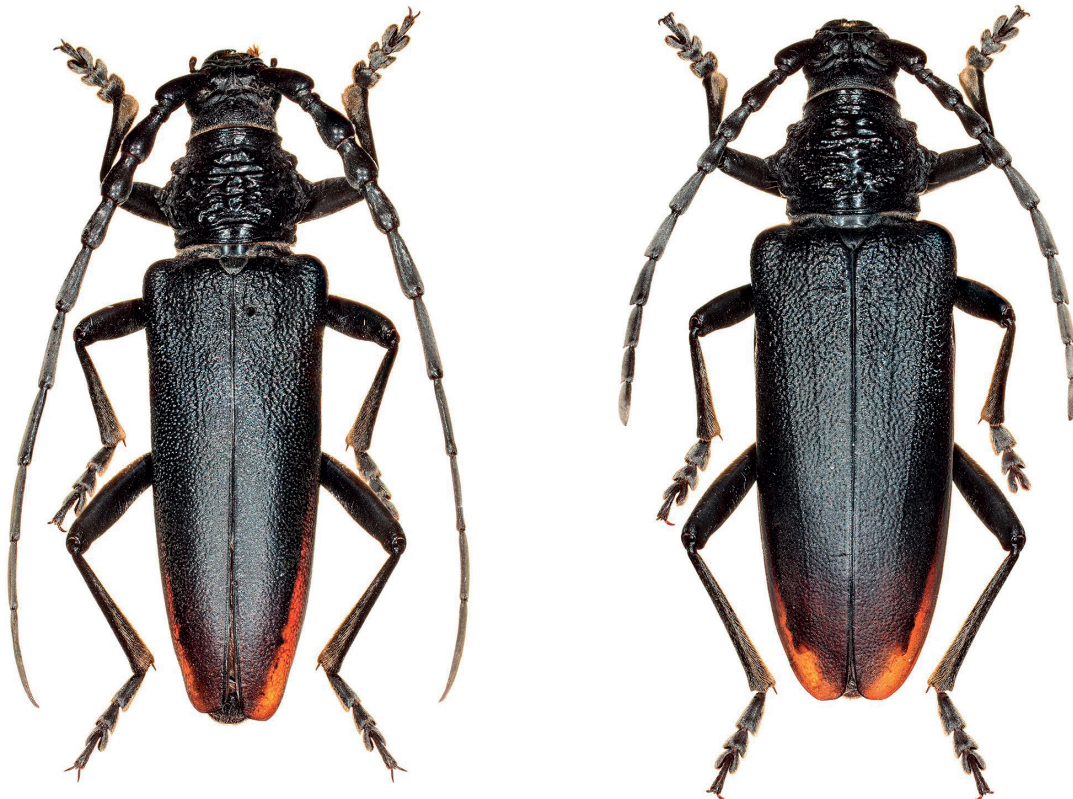


Fig. S1 – Male (left) and female (right) specimens of *Cerambyx miles*.

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